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Two new species and a new record of hydroids (hydrozoa: hydroidolina) from Port Phillip, Australia

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Abstract

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A hydroid colony from Port Phillip, southern Australia, yielded two new species, *Sertularella eleganta* and *Bimeria lutea* and a new record of *Campanularia laminocarpa* Millard, 1966, previously known from South Africa. Four other known species were epizoic on *Sertularella eleganta*.

Keywords

Southern Australia, Port Phillip, *Sertularella eleganta* sp. nov., *Bimeria lutea* sp. nov., *Campanularia laminocarpa* Millard, 1966.

Introduction

A collection of hydroids made using scuba from the jetty at the historic site of South Channel Fort in Port Phillip, southern Australia, yielded a colony of a new species of *Sertularella* (*S. eleganta*), a new species of *Bimeria* (*B. lutea*) and a new record of *Campanularia laminocarpa* Millard, 1966, previously known from South Africa. Other species sparsely epizoic on the colony of *S. eleganta* were *Clytia hemisphaerica* (Linnaeus, 1767), *Obelia dichotoma* (Linnaeus, 1758), *Monothecha flexuosa* (Bale, 1894) and *Lafoeina amirantensis* (Millard and Bouillon, 1973).

The new species and new record are described. Type and voucher material is lodged in Museum Victoria (NMV F).

Sertularella Gray, 1847

Diagnosis. (Bouillon *et al.*, 2006). Colony erect, branched or unbranched, monosiphonic or polysiphonic, hydrocaulus and hydrocladia when present, with two longitudinal rows of hydrothecae, hydrothecal margin with four cusps, submarginal teeth present or absent, operculum pyramidal, composed of four triangular valves, retracted hydranth with abcauline caecum, gonophores as solitary fixed sporosacs, acrocysts in some species.

Sertularella eleganta sp. nov.

Figure 1A–F

Material examined. NMV F228240, holotype, colony initially 5% formalin preserved later transferred to alcohol; fertile colony on rock

in crevice 1m deep, coll: J.E.Watson, 22/3/2016. NMV F228241, microslide malinol mounted, from holotype colony.

Description. Hydrorhiza comprised of narrow stolon tubes reptant on concrete surface. Colony without definite main stem, branching from base, branches monosiphonic except proximally where some are lightly fascicled from upward-growing stolons which become primary branches. Branches straight, secondary branches given off irregularly from primaries below a hydrotheca at an angle of c. 45°. Branch internodes variable in length, an indistinct oblique node at junction of adnate and free hydrothecal adcauline wall, marked by an indentation and narrowing of perisarc. Proximal internode of secondary branch cylindrical, long to first hydrotheca.

Hydrothecae alternate, tubular, widely separated along branches, set at an angle of 40–50° to internodal axis, walls smooth, narrowing from base to margin. Hydrotheca widest at junction of adnate and free adcauline wall, adnate adcauline wall almost parallel to internodal axis, free adcauline wall slightly concave to straight, ratio of length of adnate to free adcauline wall 1:2, abcauline wall weakly convex to straight. Floor of hydrotheca short, transverse to internode with a small central foramen. Margin delicate with four equidistant cusps with shallow embayments between and four large thin internal submarginal cusps of similar shape and size below margin. Operculum of four very thin flaps. Hydranth too decomposed for description.

Gonothecae borne abundantly along lower to mid sections of branches, inserted singly on a short unsegmented pedicel

opposite a hydrotheca, facing obliquely upwards. Body of mature gonotheca elongate oval, variable in length with three to five broad corrugations, obscure proximally becoming more prominent distally, surmounted by a long narrow neck above distalmost deep corrugation, with four equidistant very long, sharp, often inwardly curved apical spines. Gonophores female, some extruded from gonotheca as acrocysts.

Perisarc moderately thin throughout. Colour in life pale yellowish-grey, stolons pale brown.

Table 1. Measurements (μm) of *Sertularella eleganta*

| Branch | |
|-------------------------------------|-----------|
| internode length | 520-800 |
| width at node | 160-184 |
| length to first secondary internode | 700-1000 |
| Hydrotheca | |
| length of abcauline wall | 440-480 |
| length of adnate adcauline wall | 280-320 |
| length of free adcauline wall | 576-650 |
| width at margin | 192-208 |
| Gonotheca | |
| length overall | 1400-1740 |
| maximum width | 680-880 |
| length of neck | 296-360 |
| width of neck | 168-232 |
| length of apical spines | 72-96 |

Remarks. The colony was growing in a sheltered crevice between concrete jetty footings in an oceanic strong current-flow habitat. The delicate flexuous perisarc suggests a deep water species. Many hydrothecae are infested with one or two large crustacean eggs.

The nearest congeners of *Sertularella eleganta* are *Sertularella robusta* Coughtrey 1876 and *Sertularella natalensis* Millard, 1968. *Sertularella. robusta* is a very common southern Australian species occurring in the same habitat as *Sertularella eleganta* in Port Phillip. While similar to *S. robusta* the hydrothecae of that species are sometimes faintly rugose, and the gonothecae is more ridged and terminal spines are shorter. Colony morphology of *S. natalensis* differs from *S. eleganta* in the ratio of fixed:free wall and in striations on the hydrothecae. Although *Sertularella* is a genus with many species, no others have the same morphological, hydrothecal and gonothecal characters as *Sertularella eleganta*.

Etymology. The species name refers to the elegantly branched colony.

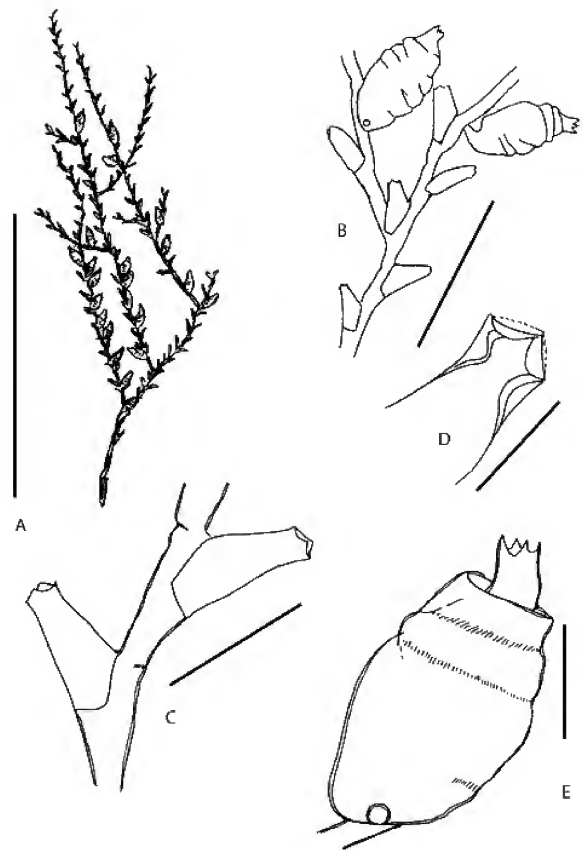


Figure 1A-E. *Sertularella eleganta* sp. nov. Holotype NMV F228241. 1A fertile branch. 1B, part of branch with gonothecae. 1C, branch internodes. 1D, submarginal hydrothecal cusps. 1E, gonotheca. Scale bar: 1A, 20 mm, 1B,C 2 mm, 1D, E, 0.5 mm.

Bimeria Wright, 1859

Diagnosis. (Bouillon *et al.*, 2006). Colony stolonal or with erect branching hydrocauli, stem with firm perisarc enveloping hydranth, extending as a pseudohydrothecal sheath over proximal portion of tentacle, hydranth ovoid to vasiform, hypostome dome-shaped, one or two close whorls of tentacles, gonophores as fixed sporosacs.

Bimeria lutea sp. nov.

Figure 2A-E

Material examined. NMV F228242 holotype, fertile colony alcohol preserved, epizoic on *Sertularella eleganta*, 1m deep, coll: J.E.Watson, 22/3/2016. NMV F228243, malinol mounted microslide from holotype colony.

Description. Colonies fertile, borne abundantly on lower branches of *Sertularella eleganta*. Hydrorhiza of tubular stolons reptant on host colony. Hydrocauli straggling, hydranths

borne on single pedicels or on sparsely and irregularly branched stems to 4–5 mm long (rarely 8 mm long). Stems and pedicels monosiphonic, thick, of same diameter as stolons, deeply annulated above junction with stolon and above and below each branch, annulations often fading into corrugations before becoming smooth. Branching predominantly of first order, occasionally second order.

Hydrothecae terminal on pedicels of variable length, hydrotheca vasiform (preserved), a pseudohydrotheca covering body, hypostome dome-shaped with 10–12 finger-shaped tentacles arranged in an untidy whorl below hypostome (live material), the pseudohydrotheca continuing as a thin gelatinous pellicle over proximal region of tentacles.

Gonophores male, elongate oval, arising singly on a short annulated pedicel from stem and branches, enclosed in a thick gelatinous sheath, spadix central, leaf-shaped, opaque.

Cnidome (from live material) clusters of nematocysts of two categories in transverse bands along tentacles, none discharged:

- microbasic euryteles, loaf-shaped, 4–5 x 8.5–9 μm ,
- desmonemes, droplet-shaped, 4 x 6 μm .

Perisarc very thick on proximal stem region; hydrocaulus, hydranth and gonophores invested with very fine sediment. Colour of colony in life: stolons pale brown, hydrocaulus and tentacles white, hypostome yellow, spadix of gonophore brown.

Table 2. Measurements (μm) of *Bimeria lutea*

| | |
|----------------------|----------|
| Stolon, branch width | 48–72 |
| Hydranth | |
| length of pedicel | 200–2000 |
| length of body | 160–180 |
| maximum width | 160–184 |
| Gonophore | |
| length of pedicel | 64–80 |
| length | 360–400 |
| maximum width | 112–200 |

Remarks. *Bimeria* is a genus of nine species (Bouillon *et al.* 2006), two of which are known from Australia. *Bimeria australis* Blackburn 1937 (redescribed by Watson 1978) is from the same southern Australian locality as *B. lutea*, and *Bimeria currumbensis* Pennycuik, 1959 is from tropical southern Queensland. The morphology of *B. lutea* fits with neither Australian species. Colonies of *B. australis* are not as abundantly rampant as those of *B. lutea*; they are buff-coloured with a wrinkled hydrocaulus and the stems stand erect from the substrate. *B. currumbensis* described from meagre infertile material by Pennycuik (1959) is a much larger species and lacks an annulated hydrocaulus.

Bimeria vestita Wright, 1859 is a known epizoite of sertulariid hydroids and has been described by Millard (1975), Calder (1988) and Migotto (1996); the type material was

re-examined by Marques *et al.* (2000). Differences between the various descriptions are such that it is likely that more than one species may be involved. The type as described by Marques *et al.* (2000) is much larger and more branched than *B. lutea*, the number of tentacles is greater, the nematocysts are smaller (probably due to shrinkage), the pedicels widen distally and those of the gonophore are longer. Millard (1975) mentioned but did not figure a branching male spadix in *B. vestita*; her material may be a different species, possibly more closely related to *B. lutea* than to *B. vestita*.

Etymology. The species is named for the yellow colour of the hypostome.

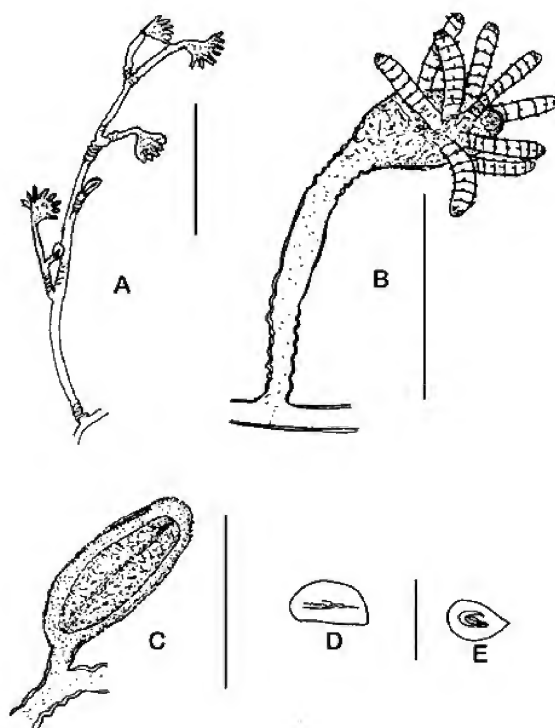


Figure 2A–E. *Bimeria lutea* sp. nov. (holotype colony NMV F228242). 2A, branched stem. 2B, pedicellate hydrotheca (from live material). 2C, male gonophore. 2D, microbasic eurytele. 2E, desmoneme. Scale bar: 2A, 2 mm. 2B, C, 0.3 mm. 2D, E, 10 μm .

Campanularia Lamarck, 1816

Diagnosis. (Bouillon *et al.* 2006). Colony stolonial, seldom erect and branched, hydrorhiza not anastomosing, hydrothecal pedicel unbranched, hydrotheca campanulate or bell-shaped with entire or cusped margin, demarcated from pedicel basally by a variously developed annular perisarcal thickening, hydrothecal walls with unthickened perisarc, not abruptly everted distally, true diaphragm absent, subhydrothecal spherule present, gonophores fixed sporosacs, gonotheca on hydrorhiza.

***Campanularia laminocarpa* Millard, 1966**

Figure 3A-E

Campanularia laminocarpa Millard, 1966: 211, fig. 67F-K
Clytia sp. Watson 1975: 158, fig. 1.

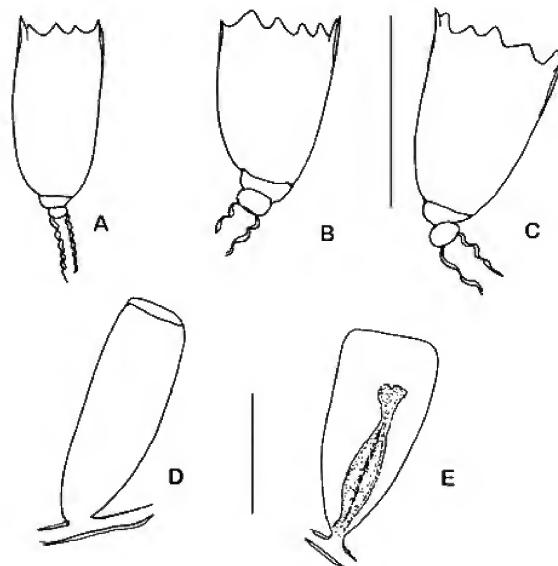
Material examined. Microslide NMV F228244, malinol mounted, from small infertile colony epizoic on *Sertularella eleganta* in crevice, 1m deep, coll: J.E.Watson, 22/3/2016. **Other Material:** NMV F228246 microslide, malinol mounted, fertile colony on *Syntheicum patulum* (Busk, 1852) on reef, North Arm Channel Western Port, 8m, coll: J.E. Watson 16/12/1996. NMV F228247 microslide, malinol mounted, fertile colony on *Syntheicum patulum*, reef, 2 km offshore from McGaurans Beach, Ninety Mile Beach, Bass Strait, 16m, coll: J.E. Watson 12/8/1983. Microslide (author's collection), malinol mounted, Fluted Cape, Tasmania, 15m deep, coll: J.E.Watson, April, 1975.

Description. Colony (NMV F228244) stolonal, hydrorhizal stolon tubular, reptant on *Sertularella eleganta*. Hydrocaulus pedicellate, unbranched, monosiphonic, pedicels variable in length and width, deeply annulated or spirally ringed throughout, rarely with smooth patches, pedicel terminating in a cushion-shaped shoulder supporting a spherule. Hydrotheca proximally narrow with a moderately long subhydrothecal chamber with shallow perisarc distal ring, walls then widening to become parallel, sometimes expanding, circular in section. Margin not everted, with 8-10 long cusps separated by moderately deep and wide embayments, a slight thickening of perisarc below margin.

Gonothecae male [Western Port (NMV F228246) and Bass Strait (NMV F228247)], very large, campanulate, flattened, borne from hydrorhiza on a short unsegmented pedicel, held obliquely away from host, perisarc smooth without ornamentation, aperture occupying entire distal margin, sealed by a thin dome-shaped operculum torn aside at maturity. Perisarc thin and transparent throughout, gonothecha fragile and easily collapsed.

Remarks. I have compared several specimens of *Campanularia* epizoic on *Syntheicum patulum* (Busk, 1852) collected over many years of scuba diving from the southern Australian localities of Western Port, Bass Strait and Tasmania with a specimen *Campanularia laminocarpa* Millard, 1966 (gift to author from Millard in 1985). Although the size, shape and dentition of the hydrotheca varies within Australian localities, morphology and dimensions of the gonothecae clearly establishes the Australian material as *C. laminocarpa*. Minor morphological differences between the South African and Australian material such as hydrothecal marginal replication of the South African species replaced by submarginal thickening in the Australian material may be due to environmental factors or colony maturity. The weak perisarc thickening at the junction of the subhydrothecal chamber with the body, commented upon by Millard (1966), is present in some Australian hydrothecae and can be mistaken for a diaphragm (see Watson 1975: 158). The hydrothecal margins of the present specimens of *C. laminocarpa* are very fragile and easily collapsed, resulting in changes in apparent shape of the cusps in mounted specimens.

The small infertile colony on branches of the *Sertularella eleganta* host is intergrown with *Clytia hemisphaerica*.

Table 3. Measurements (μm) of *Campanularia laminocarpa*

| | |
|---------------------------------|-----------|
| Pedicel | |
| length | 400-680 |
| width | 36-40 |
| Hydrotheca | |
| length overall | 368-464 |
| width at margin | 128-168 |
| width at diaphragm | 44-56 |
| depth of subhydrothecal chamber | 36-40 |
| diameter of spherule | 40-44 |
| length of cusp | 40-48 |
| Gonothecha | |
| length including pedicel | 1400-2000 |
| width of margin | 800-900 |

Figure 3A-E. *Campanularia laminocarpa*. 3A (NMV F228244), hydrotheca from *Sertularella eleganta*, South Channel Fort. 3B, hydrotheca (NMV F228246) from colony on *Syntheicum patulum*, North Arm Channel, Western Port. 3C, hydrotheca (NMV F228247) from colony on *Syntheicum patulum*, off Ninety Mile Beach, Bass Strait. 3D, E, gonothecae from colony, Ninety Mile Beach, Bass Strait. Scale bar: 3A-C, 0.3 mm. 3D, E, 1.0 mm.

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The sea cucumbers of Camden Sound in northwest Australia, including four new species (Echinodermata: Holothuroidea)

(<http://zoobank.org/urn:lsid:zoobank.org:pub:A7209365-ACCA-4E42-A11F-D211FF09EFD8>)

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Abstract

O'Loughlin P.M., Harding, C. & Paulay, G. 2016. The sea cucumbers of Camden Sound in northwest Australia, including four new species (Echinodermata: Holothuroidea). *Memoirs of Museum Victoria* 75: 7–52.

All sea cucumbers collected from Camden Sound by the *Kimberley Marine Research Program* in 2015 are reported, with live colour illustrations of the species. Four new species are described, with O'Loughlin as author: *Holothuria* (*Metriatyla*) *keesingi*; *Neothyonidium* (?) *insolitum*; *Plesiocolochirus minaeus*; *Protankyra torquea*. *Colochirus quadrangularis* Troschel, the type species of *Colochirus* Troschel, is reviewed and a *sensu stricto* diagnosis is provided for *Colochirus*. *Plesiocolochirus spinosus* (Quoy & Gaimard), the type species of *Plesiocolochirus* Cherbonnier, is reviewed and a *sensu stricto* diagnosis is provided for *Plesiocolochirus*. *Colochirus robustus* Östergren is confirmed for NW Australia, but not for Camden Sound. *Pseudocolochirus axiologus* (H. L. Clark) is raised out of synonymy with *Pseudocolochirus violaceus* (Théel). *Thyone papuensis* Théel is reported from Camden Sound and the species is reviewed and illustrated. We report *Thyone pedata* Semper from Joseph Bonaparte Gulf in northern Australia, but not for Camden Sound. The WA Naturalists Club visited “Camden Harbour” in 1990 and Marsh reported on the marine invertebrates. Two sea cucumber species from this report are included here. A phylogenetic tree is provided with sequences for species of *Colochirus* and *Plesiocolochirus*. A table is provided with a list of all sea cucumbers collected from Camden Sound. Tissue samples for genetic analysis were taken from all specimens, and tissue data are listed in two tables. Two Pilumnidae crabs were found in the coelom of the new species *Plesiocolochirus minaeus*.

Keywords

Kimberley; Camden Sound; *Colochirus*; *Metriatyla*; *Neothyonidium*; Pilumnidae; *Plesiocolochirus*; *Protankyra*; *Pseudocolochirus*; *Thyone*.

Introduction

Camden Sound, in the Kimberley Region of northwest Western Australia, is southwest of Augustus Island (–15.40 124.63) and west of Kuri Bay and Brecknock Harbour (“Camden Harbour”). In 2012 the Western Australia State Government created the *Camden Sound Marine Park*. Subsequently the *Western Australian Marine Science Institution* informs the management and monitoring of the Region through the *Kimberley Marine Research Program*. A ship-based expedition to Camden Sound was conducted in March 2015 under the auspices of WAMSI's Kimberley Benthic Biodiversity Project using AIMS's RV *Solander* and CSIRO's RV *Linnaeus*. All holothuroid echinoderm (sea cucumber) specimens were sent to Museum Victoria for determination, and the collection is the subject of this report. Colour photographs of live sea cucumber specimens were taken

during the KMRP expedition, principally by John Keesing (CSIRO), and photographs of all the species are published in this work. The Camden Sound sea cucumber collections are lodged in the Western Australian Museum.

The WA Naturalists Club visited “Camden Harbour” in 1990. Marsh (2011) reported on the marine invertebrates. Holothuroid species from Adele Island and Montgomery Reef were reported but both locations are remote from Camden Sound. The two species collected from Slate Island at the southern edge of Camden Sound are included in this work: *Holothuria* (*Halodeima*) *atra* Jaeger, 1833; *Holothuria* (*Mertensiothuria*) *leucospilota* (Brandt, 1835).

We note that the ICZN (Opinion 417, 42 pp., 1956) rejected for nomenclatorial purposes the publication by Oken 1815, and as a consequence the genera *Psolus* Oken, 1815 and *Thyone* Oken, 1815 became invalid. The Commission has now ruled in

Table 1. Sea cucumber species collected from Camden Sound.

| Order | Family | Subfamily | Taxon |
|---------------|------------------|----------------|---|
| Aspidochirota | Holothuriidae | | ¹ <i>Holothuria</i> (<i>Halodeima</i>) <i>atra</i> Jaeger, 1833 (Slate Island; WAM Z58692) |
| | | | ¹ <i>Holothuria</i> (<i>Mertensiothuria</i>) <i>leucospilota</i> (Brandt, 1835) (Slate Island; WAM Z58735) |
| | | | <i>Holothuria</i> (<i>Metriatyla</i>) <i>keesingi</i> O'Loughlin sp. nov. |
| | | | <i>Holothuria</i> (<i>Thymiosycia</i>) <i>gracilis</i> Semper, 1868 |
| | Stichopodidae | | <i>Stichopus</i> unresolved species complex including <i>Stichopus herrmanni</i> Semper, 1868 |
| Dendrochirota | Cladolabidae | | <i>Globosita elnaeae</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel 2014) |
| | Cucumariidae | Colochirinae | <i>Cercodemas anceps</i> Selenka, 1867 |
| | | | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| | | | <i>Leptopentacta grisea</i> H. L. Clark, 1938 |
| | | | <i>Plesiocolochirus</i> sp. 1, unresolved species complex including <i>P. australis</i> (Ludwig, 1875) |
| | | | <i>Plesiocolochirus minaeus</i> O'Loughlin sp. nov. |
| | | | <i>Pseudocolochirus axiologus</i> (H. L. Clark, 1914) |
| | Phyllophoridae | | <i>Phyllophorus</i> (<i>Urodemella</i>) <i>holothurioides</i> Ludwig, 1875 |
| | | | <i>Phyllophorella spiculata</i> (Chang, 1935) |
| | Sclerodactylidae | | <i>Havelockia versicolor</i> (Semper, 1867) |
| | Thyonidae | Semperiellinae | <i>Massinium bonapartum</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| | | | <i>Neothyonidium</i> (?) <i>insolitum</i> O'Loughlin sp. nov. |
| | | Thyoninae | <i>Hemithyone semperi</i> (Bell, 1884) |
| | | | <i>Stolus canescens</i> (Semper, 1867) |
| | | | <i>Thyone papuensis</i> Théel, 1886 |
| | Thyonidiidae | | <i>Actinocucumis longipedes</i> H. L. Clark, 1938 |
| | | | <i>Actinocucumis solanderi</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| | | | <i>Actinocucumis typica</i> Ludwig, 1875 |
| | | | <i>Mensamaria intercedens</i> (Lampert, 1885) |
| Molpadida | Molpadiidae | | <i>Molpadia scabrum</i> (Sluiter, 1901) |
| Synaptida | Synaptidae | Rynkatorpinae | <i>Protankyra insolens</i> (Théel, 1886) |
| | | | <i>Protankyra torquea</i> O'Loughlin sp. nov. |
| | | | <i>Protankyra verrilli</i> (Théel, 1886) |
| | | Synaptinae | <i>Synaptula lamperti</i> Heding, 1928 |
| | | | <i>Synaptula recta</i> (Semper, 1867) |

¹WAM specimens collected at Slate Island by WANC in July 1990, and reported by Marsh (2011).

favour of their availability (Opinion 2367) in response to an application to the ICZN by Paulay & O'Loughlin (Case 3598) for both *Psolus* Oken, 1815 and *Thyone* Oken, 1815 to be made available.

Abbreviations

AIMS Australian Institute of Marine Science
 CSIRO Commonwealth Scientific and Industrial Research Organization
 GA Geoscience Australia

KMRP Kimberley Marine Research Project
 LKCNHM Lee Kong Chian Natural History Museum
 MOL AF Prefix for code number of tissues provided to the University of Florida for sequencing
 MRAC Royal Museum for Central Africa, Tervuren
 NMV Museum Victoria, with specimen registration prefix F
 NUS National University of Singapore
 PH University of the Philippines
 PMCP Pilbara Marine Conservation Program

| | |
|---------|--|
| TMSI | Tropical Marine Science Institute (Singapore) |
| UF | University of Florida |
| USNM | United States National Museum (Smithsonian Institution) |
| WAM | Western Australian Museum, with specimen registration prefix Z |
| WAMSI | Western Australian Marine Science Institution |
| WANC | The Western Australian Naturalists Club |
| ZRC | Zoological Reference Collection of LKCNHM |
| ZRC.ECH | LKCNHM catalogue number prefix (echinoderms) |

Methods.

All specimens were preserved in 100% ethanol on the vessel by WAM staff, and databasing and weighing of specimens was done by CSIRO. The colour photos of live specimens published here were taken at the time of collection, principally by John Keesing (CSIRO) using a Nikon D300 digital SLR camera. Some specimens were photographed without a scale. We have estimated that there is about 25% shrinkage of soft-bodied specimens when preserved in 100% ethanol, and no shrinkage in hard-bodied specimens. We have thus been able to provide an estimated live colour size in the captions when there is no scale bar for the live photos of the now preserved specimens. Most of the macro images of preserved specimens were taken by Caroline Harding, with Mark O'Loughlin, using a Canon 5D mark ii camera mounted on a camlift Visionary Digital auto stepper. A Zerene Image Stacker, Adobe Lightroom and Photoshop were used for image processing and editing. Macro images of the preserved holotype of *Neothyonidium*(?) *insolitum* were taken by Melanie Mackenzie (NMV) with a Leica DC500 high resolution digital camera system with Auto Montage software. The photos of ossicles were taken by Caroline Harding, with Mark O'Loughlin, using a LEICA DM5000 B microscope, Leica application software, and Helicon Focus montage software.

Tissues were sent to Gustav Paulay (UF) for sequencing, and specimen source locations, tissue codes, catalogue numbers and GenBank Accession numbers are recorded in Appendices 1 and 2. A 655 bp portion of the mitochondrial gene cytochrome oxidase subunit 1 (COI) was sequenced from selected specimens using the echinoderm barcoding primers COIceF (5'-ACTGCCACGCCCTAGTAATGATATTTTTT ATGGTNATGCC-3') and COIceR (5'-TCGTGTGTCTACGT CCATTCCTACTGTRAACATRTG-3') (Hoareau & Boissin 2010), as described in Michonneau & Paulay 2014. We note that these echinoderm specific primers amplify positions 242 to 898 in COI compared with positions 74 to 733 amplified by Folmer primers. COI sequences were aligned by eye and analyzed using Maximum Likelihood with 100 bootstrap replicates, implemented in MEGA 6.06 (Tamura *et al.* 2013). Sequences have been submitted to GenBank (See Appendix 2).

Terminology.

For small concave plates, with two large central and two smaller distal perforations, and sometimes with additional small outer perforations, we use the term bowl, not cup or basket.

Order **Aspidochirotida** Grube, 1840

Holothuriidae Burmeister, 1837

Holothuria (*Metriatyla*) Rowe, 1969

Holothuria (*Metriatyla*) *keesingi* O'Loughlin sp. nov.

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:ED316CAC-695D-4EB7-97DD-8999F2CD33CF>

Table 1; appendix 1; figures 2a, b, 3, 4

Material examined. Holotype. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_47, WAM station no 42, barcode 10002938, from -15.612805 124.073033 36 m to -15.612437 124.072883 35 m, 26 Mar 2015, WAM Z89006.

Paratypes. Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_107, WAM station no 1, barcode 10000043, from -15.514826 124.183111 46 m to -15.514503 124.183774 45 m, 14 Mar 2015, WAM Z89000 (1 specimen); RV *Solander*, sled, site no SOL_8, WAM station no 7, barcode 10000403, from -15.313929 124.112518 47 m to -15.313336 124.111992 48 m, 16 Mar 2015, WAM Z89001 (3); RV *Solander*, sled, site no LIN_36, WAM station no 17, barcode 10001168, from -15.220444 124.320894 50 m to -15.220159 124.320648 50 m, 18 Mar 2015, WAM Z89002 (2); RV *Solander*, sled, site no SOL_32, WAM station no 19, barcode 10001320, from -15.253592 124.203038 45 m to -15.253318 124.202302 45 m, 19 Mar 2015, WAM Z89003 (1); RV *Solander*, sled, site no SOL_24, WAM station no 23, barcode 10001821, from -15.40642783 124.1259284 42 m to -15.40693704 124.1253687 42 m, 20 Mar 2015, WAM Z89004 (2); RV *Solander*, sled, site no SOL_87, WAM station no 24, barcode 10001954, from -15.448727 124.153629 36 m to -15.44933 124.154105 36 m, 20 Mar 2015, WAM Z89005 (2); RV *Solander*, sled, site no SOL_47, WAM station no 42, barcode 10002963, from -15.612805 124.073033 36 m to -15.612437 124.072883 35 m, 26 Mar 2015, WAM Z89007 (1).

Description (preserved in 95% ethanol). Up to 60 mm long, 18 mm wide, 12 mm high; body surface finely nodulose; body arched dorsally, with rounded ventro-lateral margins, low convex ventrally; strongly tapered anteriorly and posteriorly; dorsal and lateral papillae irregularly distributed, conical, with tapered to pointed ends, of variable sizes, up to 3 mm long; about eight papillae across body transversely, longest on dorso-lateral radii, about 40 ventro-lateral papillae in close irregular series on each margin; tube feet digitiform, up to 2 mm long, scattered on ventrum but in recognizable irregular longitudinal series, paired irregular series latero-ventrally, paired irregular series on each side of bare mid-ventrum; mouth antero-ventral, with 20 tentacles, mouth surrounded by a ring of about 16 conical papillae, up to 1 mm long; calcareous ring solid, widths of radial and inter-radial plates sub-equal, inter-radials half the height of the radials, with undulating posterior edge, lacking posterior prolongations.

Body wall ossicles large tables and buttons, buttons more abundant than tables; table discs of variable size, shallow concave, irregularly round to rounded square to oval, margin smooth, discs 48–240 μ m across, disc perforations from 8 to more than 50, perforations very small marginally; table spires of variable height, up to 176 μ m long, 4 pillars, up to 8 cross bridges, spire rounded distally with cluster of small spinelets, sometimes spinelets extend along distal sides of spire; buttons

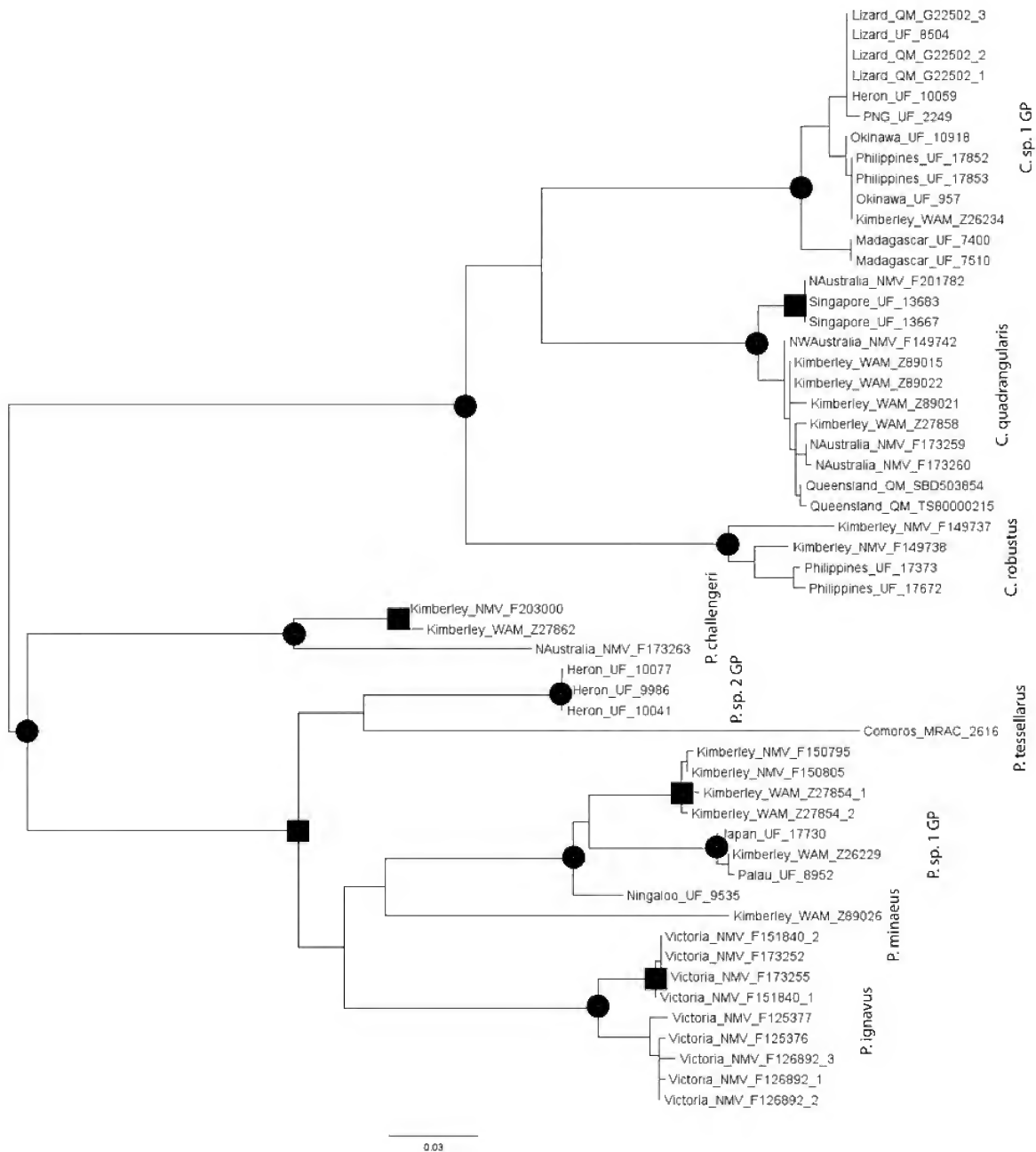


Figure 1. Maximum likelihood tree of *Colochirus*-*Plesiocolochirus* COI data, with mid-point rooting. Bootstrap support (100 replicates) indicated by circles (100%) and rectangles (>95%).

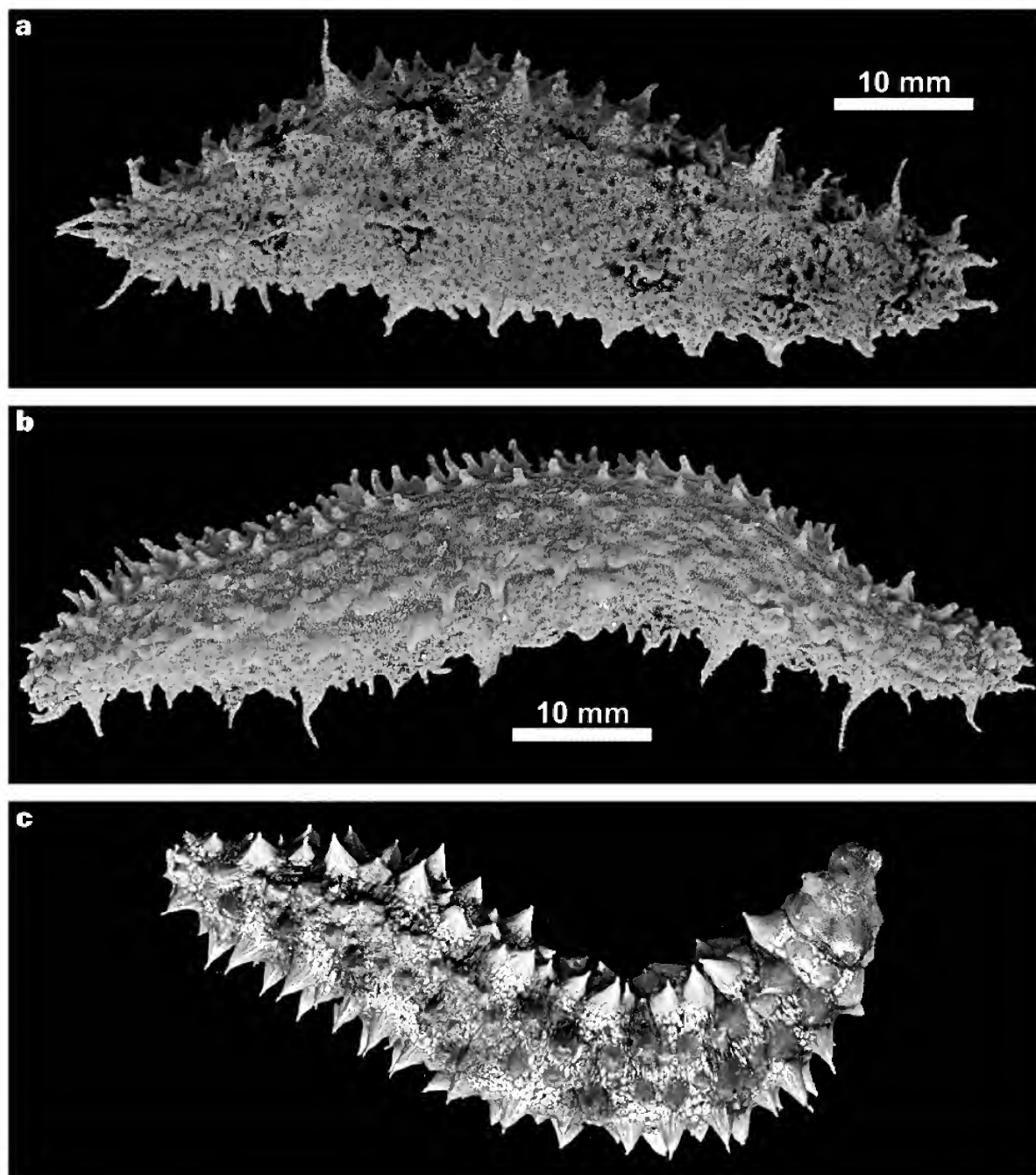


Figure 2. a, b, photos of live holotype specimen of *Holothuria (Metriatyla) keesingi* O'Loughlin sp. nov. (WAM Z89006): a, dorso view; b, latero-ventral view with ventrum and tube feet along upper side, dorsal papilla underneath. c, photo of dorsal view of live specimen of *Holothuria (Thymiosycia) gracilis* Semper, 1868 (WAM Z89008; estimated 125 mm long live).

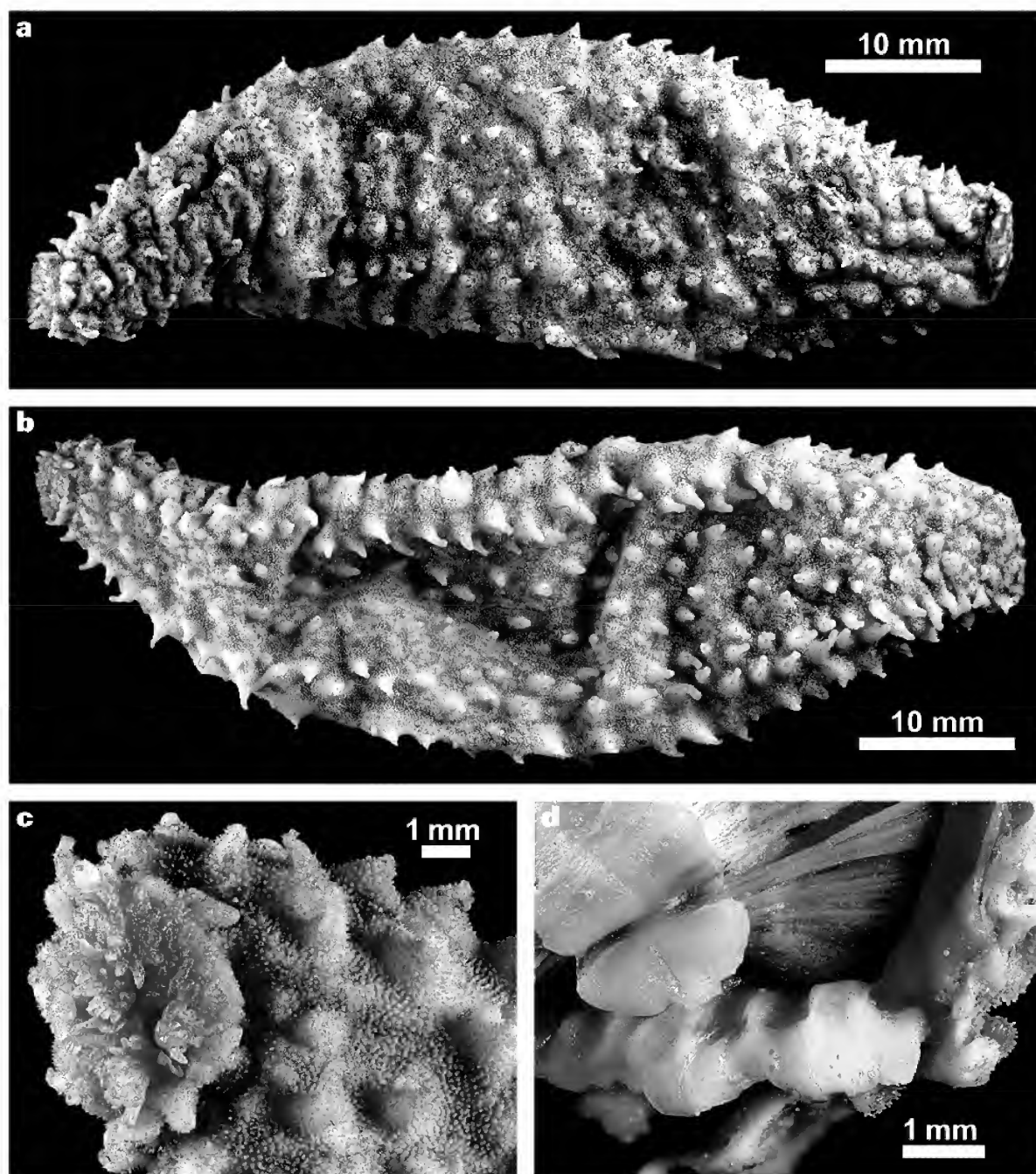


Figure 3. Preserved holotype of *Holothuria (Metriatyla) keesingi* O'Loughlin sp. nov. (WAM Z89006): a, dorsal view; b, ventral view; c, tentacles with surrounding ring of papillae; d, calcareous ring with radial plate right, inter-radial plate left.

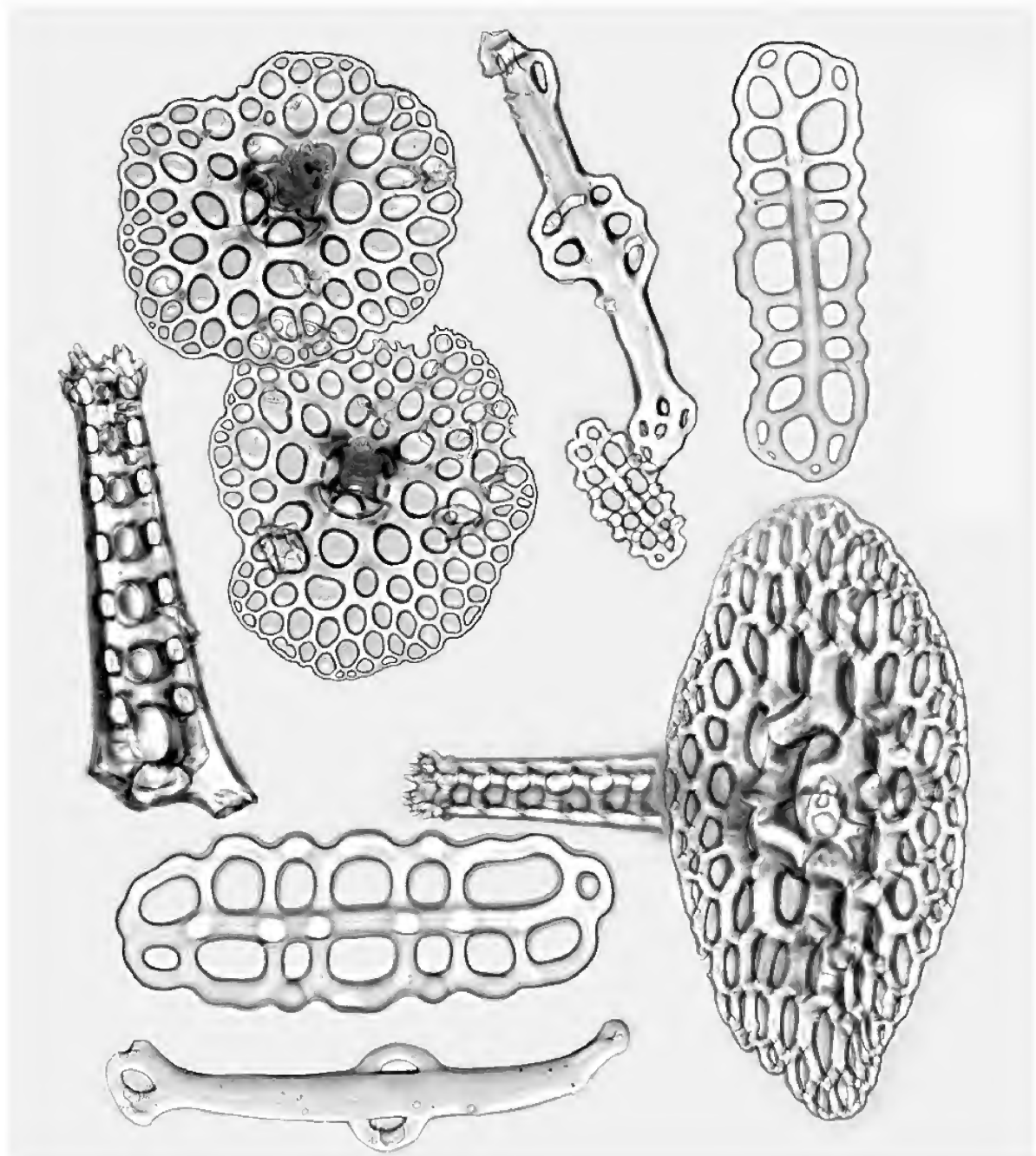


Figure 4. Ossicles from holotype (WAM Z89006; rods and small button mid-top and bottom) and paratype (WAM Z89005; tables, buttons) specimens of *Holothuria (Metriatyla) keesingi* O'Loughlin sp. nov. (in specimens table discs up to 240 μm across; table spires up to 176 μm long; buttons up to 200 μm long; rods up to 336 μm long).

predominantly elongate with up to about 7 irregularly paired perforations, some buttons with 1–3 pairs of perforations, button sizes 50–200 μm long, buttons smooth and variably knobbed. Dorsal papillae with tables, buttons and thick perforated rods; rods thick, mid-rod widened with perforations, distal ends widened with small perforations, rods up to 336 μm long. Ventral tube feet with endplates, thick endplate support rods, tables and buttons; endplates slightly convex, central perforations slightly larger, margin bluntly digitiform, endplate diameters about 300 μm ; thick rods curved, widened and perforated mid-rod and distally, up to 264 μm long. Tentacles with minutely spinous, non-perforate, curved rods, rods up to 320 μm long.

Colour (preserved). Body pale mottled brown to off-white, dorsal and lateral irregular fine brown-black flecks and spots, about 4 dorso-lateral pairs of large irregular brown-black patches that are partly merged at the anterior end; tentacles and distal papillae and tube feet yellow. Live colour similar but the body base colour yellow.

Distribution. NW Western Australia, Kimberley Region, Camden Sound, mud, 35–50 m.

Etymology. Named for John Keesing of the CSIRO Oceans and Atmosphere, and The Western Australian Marine Science Institution, with appreciation of his live colour photography of Camden Sound sea cucumbers used in this work, and his gracious collaboration with data.

Remarks. The morphology of *Holothuria (Metriatyla) keesingi* O'Loughlin sp. nov. satisfies the diagnosis of the *Holothuria* sub-genus *Metriatyla* Rowe, 1969:

1. 20 tentacles;
2. collar of papillae around the base of the tentacles;
3. large conical, irregularly arranged papillae dorsally, a lateral flange sometimes evident;
4. tube feet irregularly arranged on the ventrum;
5. body arched dorsally, flattened ventrally;
6. size small to large;
7. body wall thin to thick;
8. calcareous ring well developed;
9. table ossicles with smooth disc and spire of moderate height to high, terminating in a few to many small spines;
10. buttons simple, with moderate-sized irregularly arranged knobs and 3–10 pairs of relatively large holes.

We qualify the diagnostic characters of Rowe (1969) to include the possibility of species with a large body and thick body wall (as in *Holothuria (Metriatyla) scabra* Jaeger, 1833).

Rowe (in Rowe & Gates 1995) synonymised *Holothuria bowensis* Ludwig, 1875 (type from Bowen, NE Australia) and *Holothuria subverta* H. L. Clark, 1921 (type from Torres Strait, NE Australia) with *Holothuria (Metriatyla) martensii* Semper, 1868 (type from Amboina, Indonesia). Of the species referred to sub-genus *Metriatyla*, the new species resembles

Holothuria (Metriatyla) martensii. However, the new species *Holothuria (Metriatyla) keesingi* O'Loughlin is significantly different in the following ways:

1. smaller species with numerous preserved specimens up to only 60 mm long;
2. preserved colour with yellow papilla and tube foot and tentacle ends, and dorsal body with four irregular longitudinal paired dark brown patches;
3. larger tables, with discs up to more than 200 μm across, disc perforations up to more than 40, spires up to more than 150 μm high;
4. larger smooth and knobbed buttons, predominantly about 7 irregular pairs of perforations, up to 200 μm long.

Théel (1886) referred two specimens to *Holothuria (Metriatyla) martensii*, one from Indonesia and one from the Philippines. Sizes were 150 mm and 85 mm long. Buttons were up to 140 μm long. Table disc perforations were fewer than 30. Colours are described with no reference to brown dorsal patches. These morphological characters of *Holothuria (Metriatyla) martensii* (*sensu* Théel 1886) are significantly different to those of *Holothuria (Metriatyla) keesingi* O'Loughlin sp. nov.

The buttons in *H. (Metriatyla) horrida* Massin, 1987 are similar to those in *Holothuria (Metriatyla) keesingi* O'Loughlin. And the high table spires of *H. (Metriatyla) horrida* are also similar but significantly shorter (up to 120 μm long). The table discs in *H. (Metriatyla) horrida* are significantly smaller (up to 140 μm across), the table disc perforations significantly fewer (up to 16), and the colour reported as grey.

Frank Rowe (*pers. comm.*) suggested that the size and form of the ossicles in the relatively small specimens appear somewhat paedomorphic. But the mature gonads that are present confirm that the specimens are adult.

Holothuria (Thymiosycia) gracilis Semper, 1868

Table 1; appendix 1; figure 2c

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, Ngalanguru Island, 25 Mar 2015, WAM Z89008 (1).

Remarks. This species identity was established by François Michonneau (UF, *pers. comm.*).

Stichopodidae Haeckel, 1896

Stichopus sp.

Table 1; appendix 1; figure 5

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, Montgomery Island reef flat, barcode 10003037, 24 Mar 2015, WAM Z89009 (1); barcode 10003038, 24 Mar 2015, WAM Z89010 (1).

Remarks. The taxonomy of *Stichopus* is challenging today. Based on the living appearance of this animal it could represent *Stichopus horrens* Selenka, 1867, or a specimen in the

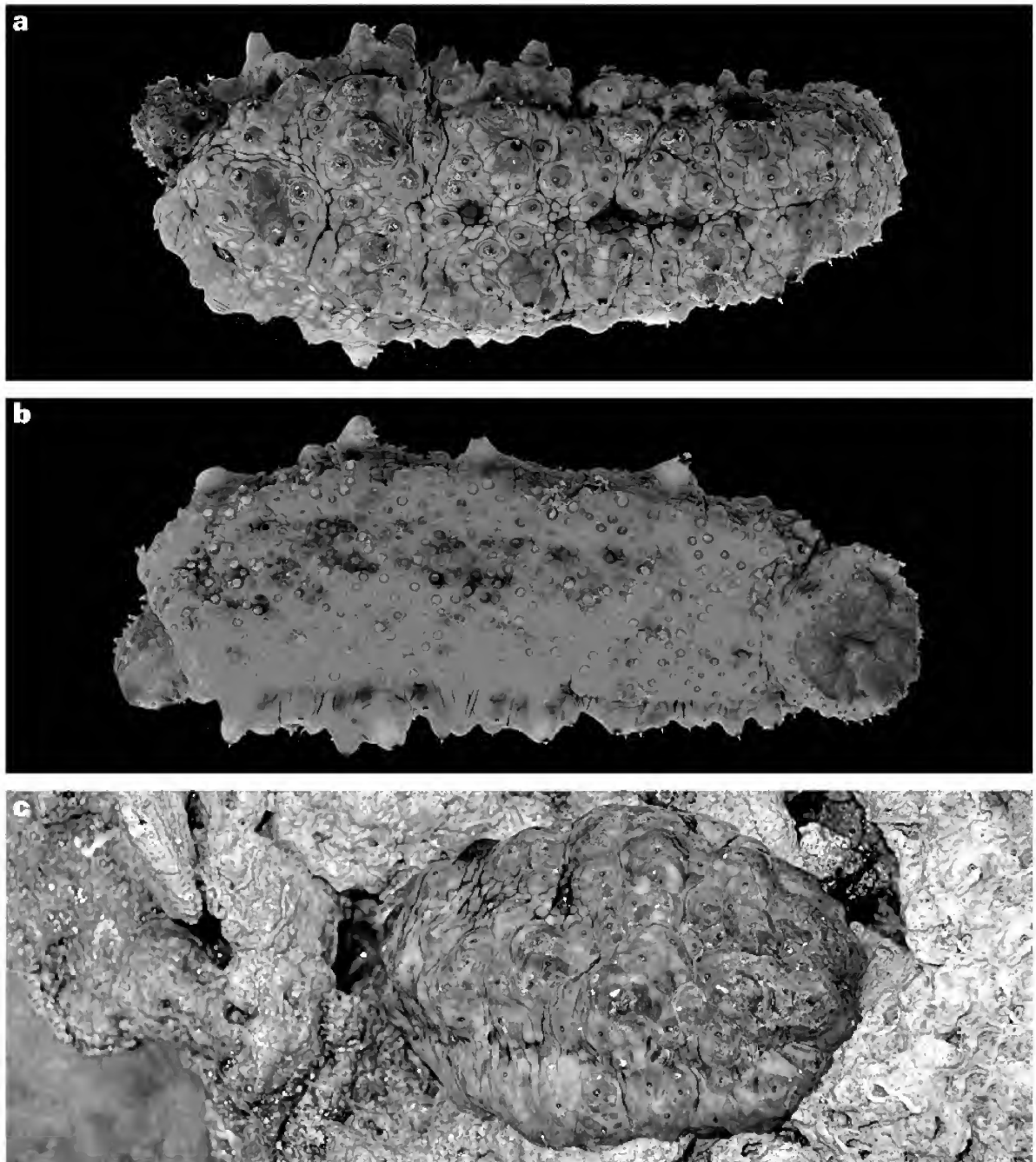


Figure 5. Photos of live specimen belonging to a *Stichopus* unresolved species complex (WAM Z89009; estimated 110 mm long live): a, dorsal view; b, ventral view; c, *in situ* view.

S. monotuberculatus (Quoy & Gaimard, 1834) or *S. herrmanni* Semper, 1868 species complexes. Specimens from NW Australia identified by Mark O'Loughlin previously as *Stichopus herrmanni* are now revised to “*Stichopus* unresolved species complex”.

Order **Dendrochirotida** Grube, 1840

Family **Cladolabidae** Heding & Panning, 1954 *sensu* Smirnov 2012

Remarks. See O'Loughlin, Mackenzie & VandenSpiegel 2014.

Globosita Cherbonnier, 1958

Remarks. See O'Loughlin, Mackenzie & VandenSpiegel 2014.

Globosita elnazae O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel 2014)

Table 1; appendix 1; figures 6a, b

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_116a, WAM station no 18, barcode 10001261, from -15.261423 124.275183 41 m to -15.261716 124.275827 40 m, 18 Mar 2015, WAM Z89011 (1); same data, barcode 10001262, WAM Z89012 (1).

Family **Cucumariidae** Ludwig, 1894

Diagnosis (after Smirnov 2012). Ten dendritic tentacles; calcareous ring lacking segmented posterior prolongations; tube feet most commonly restricted to the radii, or may also be scattered in the dorsal and lateral inter-radii; ossicles in body wall perforated plates, sometimes rods, sometimes bowls, never tables.

Subfamily **Colochirinae** Panning, 1949

Diagnosis. Cucumariidae with plate and bowl ossicles.

Cercodemus Selenka, 1867

Cercodemus Selenka, 1867: 343.—Rowe (in Rowe & Gates), 1995: 271.

Remarks. Rowe (in Rowe & Gates 1995) raised genus *Cercodemus* out of synonymy.

Cercodemus anceps Selenka, 1867

Table 1; appendix 1; figures 6c, d

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_43, WAM station no 26, barcode 10002087, from -15.488461 124.201824 46 m to -15.488309 124.201113 46 m, 21 Mar 2015, WAM Z89013 (1).

Remarks. We note that in relation to *Colochirus* Troschel, 1846 (below) and *Plesiocolochirus* Cherbonnier, 1946 (below), the monotypic *Cercodemus* Selenka, 1867 has body wall ossicles comprising deep bowls, deep bowls bridged over rim to create hollow ellipsoids, and multi-layered scales, but lacks shallow bowls and knobbed buttons.

Colochirus Troschel, 1846

Figure 1; appendices 1, 2

Colochirus Troschel, 1846: 64.—Semper, 1867: 56.—Ekman, 1918: 5–6.—Panning, 1949: 439.—Panning, 1971: 42–43, fig. 5.—Liao & Clark, 1995: 474.—Rowe (in Rowe & Gates), 1995: 272.

Type species. *Colochirus quadrangularis* Troschel, 1846 (monotypy)

Other currently assigned, accepted species (with type locality added). *Colochirus crassus* Ekman, 1918 (NW Australia; junior synonym *Colochirus quadrangularis* var. *australoides* Panning, 1949 by Rowe in Rowe & Gates 1995); *C. cylindricus* Semper, 1867 (Philippines); *C. pusillus* Helfer, 1912 (Gulf of Suez); *C. robustus* Östergren, 1898 (S Korea; junior synonym *Colochirus squamatus* Sluiter, 1901 by Rowe in Rowe & Gates 1995).

Diagnosis (sensu stricto, based on type species only, described below). Body quadrangular in mid-body section, slightly tapered towards oral and anal ends; body and papillae firm, densely packed with ossicles; preserved length up to 98 mm, dorsal and ventro-lateral radii slightly raised, each with prominent, conical papillae in irregular zig-zag rows; five oral valves, each with a terminal papilla and sometimes 1 or 2 additional papillae; five anal scales, some small peri-anal papillae, 5 longer proximal anal radial papillae. Ten dendritic tentacles, 8 large, 2 ventral small. Calcareous ring plates not forked posteriorly, lacking posterior prolongations. Dorsal and lateral inter-radii lacking tube feet; tube feet in discrete bands in ventro-lateral and mid-ventral radii, each band about 4 podia wide, ventral inter-radii usually lacking tube feet, inter-radii similar in width to the radial bands of tube feet.

Ossicles of body wall of six recognizable but inter-grading forms:

1. small, shallow bowls, margin smooth to finely knobbed or finely spinous, variably bridged across margins or not;
2. abundant rounded-rectangular to oval to irregular shallow bowls, one short or long margin prominently spinous, bowls variably partly bridged or not;
3. some rounded-rectangular to oval larger shallow bowls, sometimes partly bridged; 4. larger shallow bowls bridged on one side to create smooth, hollow, irregular ellipsoids;
5. shallow bowls, frequently thick-walled, bridged to create irregular ellipsoids with inner bridging, not hollow;
6. enlarged inner-bridged ellipsoids inter-grade with multi-layered scales.

Tentacle ossicles rod-plates, rods, rosettes.

Remarks. Rowe (in Rowe & Gates 1995) restricted *Colochirus* to three assigned species *Colochirus crassus*, *C. quadrangularis* and *C. robustus*, leaving the status of *C. cylindricus*, *C. pusillus* and *C. viridis* Semper, 1867 (considered to be *nomen dubium*) as uncertain, as they were not assigned to other genera.

With the support of CO1 sequence data (Figure 1), we confirm Ekman's report (1918) of the occurrence of *Colochirus robustus* in NW Australia.

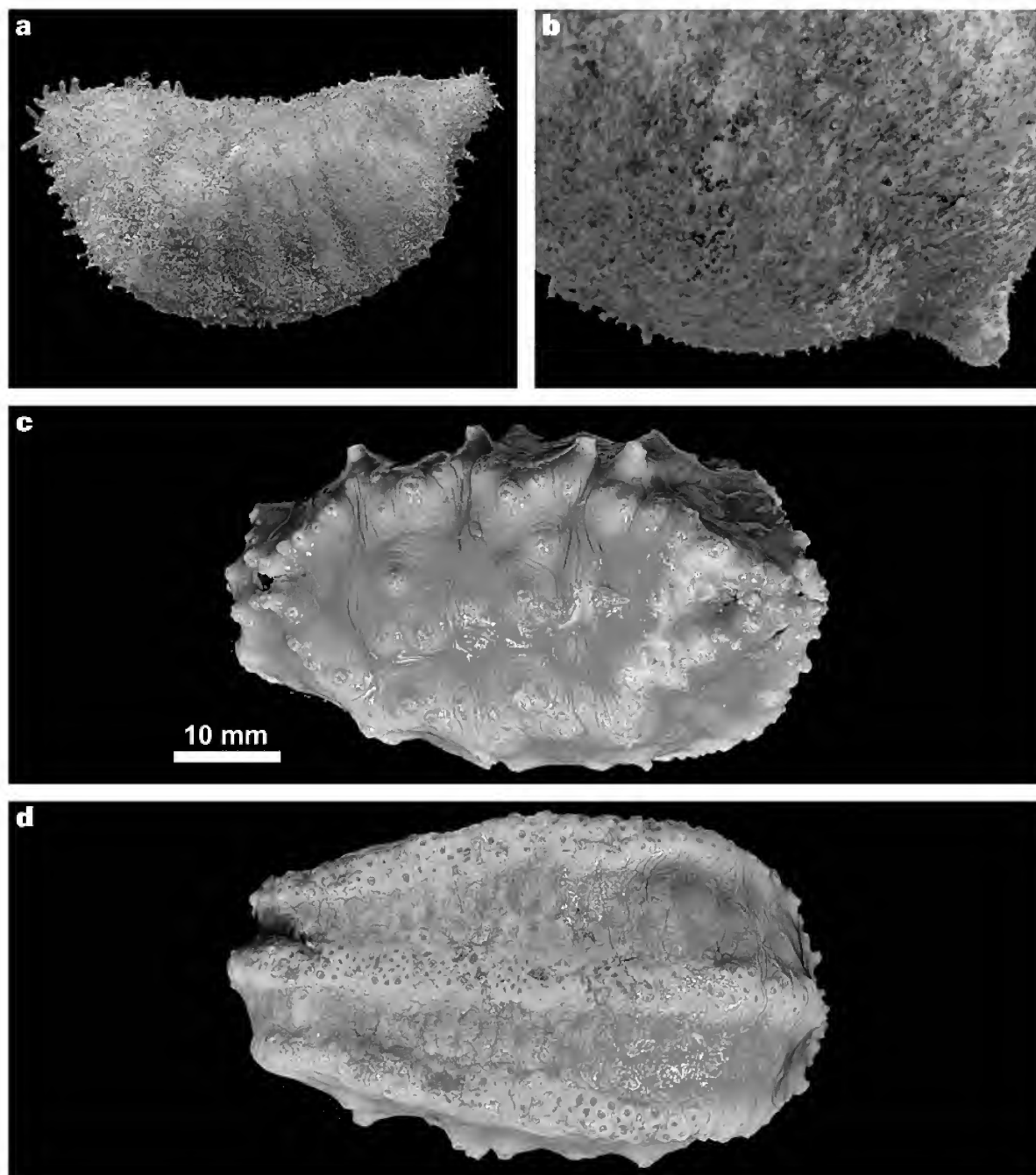


Figure 6. a, b, photos of live specimens of *Globosita elnaeae* O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel 2014): a, lateral view (WAM Z89011; estimated 25 mm long live); b, posterior dorsal view (WAM Z89012; estimated 90 mm long live). c, d, photos of live specimen of *Cercodemas anceps* Selenka, 1867 (WAM Z89013): c, dorsal view; d, ventral view.

A phylogenetic analysis based on COI sequence data shows that species currently assigned to *Colochirus* and *Plesiocolochirus* fall in two well-supported clades (Figure 1). The *Colochirus* cluster includes *Colochirus quadrangularis* (from Singapore, near the type locality, and across tropical Australia), *Colochirus robustus* (from NW Australia and the Philippines), and *Colochirus* species 1 (from N Australia, Japan, the Philippines, and Madagascar). This unassigned species is morphologically close to specimens that have frequently been identified as *Plesiocolochirus australis* (Ludwig, 1875). After examining type material, Rowe (in Rowe & Gates 1995) synonymised *Colochirus minutus* Ludwig, 1875 with *Plesiocolochirus australis* (Ludwig, 1875). We hope to examine the type specimens of both of these species and then be in a position to assign the unidentified *Colochirus* species in a subsequent work.

Panning (1971) observed that some shallow bowls (up to 107 µm long) were bridged on both sides to create irregular ellipsoids with an inner shallow bowl layer, and thus not hollow. We have not been able to support this observation by Panning (1971) as all solid ellipsoids appear to be built up on the concave side only of the shallow bowls with the outer surface supported by an inner network. Shallow bowls bridged on one side only but without an inner bridging network create irregular hollow ellipsoids. We note that *Cercodemus anceps* Selenka, 1867 has deep bowls that may be bridged to create such more regular hollow ellipsoids.

Colochirus Troschel, 1846 (type species *Colochirus quadrangularis* Troschel, 1846, above) is distinguished *sensu stricto* from *Plesiocolochirus* Cherbonnier, 1946 (type species *Plesiocolochirus spinosus* (Quoy & Gaimard, 1834), below), by:

1. absence of large imbricating external scales on distal anal cone, on proximal oral valves, and on lateral papillae;
2. absence, usually, of inter-radial tube feet;
3. absence of knobbed single-layered button ossicles in the body wall;
4. presence of tentacle rosettes.

Colochirus quadrangularis Troschel, 1846

Table 1; appendices 1, 2; figures 1, 7, 8, 9

Colochirus quadrangularis Troschel, 1846: 64–66 (*non Holothuria quadrangularis* Lesson, 1830: 90–91, pl. 31 fig. 1).—Théel, 1886: 81–82, 120–121, pl. 6 fig. 7, pl. 14 figs 7, 8.—Erwe, 1913: 353–355, fig. 2a–g.—Ekman, 1918: 21–26, pl. 1 figs 7–10, pl. 3 figs 13–15.—Panning, 1949: 446–447, figs 46, 47.—Liao & Clark, 1995: 474–475, fig. 286.—Rowe (in Rowe & Gates), 1995: 272–273.

Colochirus coeruleus Semper, 1867: 59, pl. 11 fig. 1, pl. 13 fig. 18 (synonymy by H. L. Clark 1946).

Colochirus jagorii Semper, 1867: 60.—Panning, 1971: 42 (type locality Singapore; synonymy by Rowe (in Rowe & Gates) 1995).

Colochirus tristis Ludwig, 1875: 87–88 (type locality Zanzibar; synonymy of *Colochirus jagorii* by Panning 1971).

Pentacta quadrangularis.—H. L. Clark, 1946: 391.—Cannon & Silver, 1986: 30.

Pentacta coerulea.—H. L. Clark, 1932: 227.—H. L. Clark, 1938: 449–450, pl. 16 fig. 4.

Pentacta jagorii.—H. L. Clark, 1932: 228–229.—H. L. Clark, 1946: 391–392.

Pentacta coerulea var. *rubra* H. L. Clark, 1938: 451, pl. 16 fig. 5 (single specimen from Broome, NW Australia)

Type locality. Coast of Malacca (southern region of the Malay Peninsula, near Singapore).

Material examined. Singapore, Johor Strait, dredge, channel between Beting Bronok and Chek Jawa channel, 1.41 103.98 1.5–2.4 m, mud, coll. Tan Koh Siang *et al.*, 29 Jun 2011, NMV F210388 (1) (former registration ZRC.ECH.0208; donated to Museum Victoria); west end of Jurong island (composite new island), 1.22 103.67 23.1–24.4 m, dredge, rock, sand and mud, coll. Lim Swee Cheng *et al.*, 19 Dec 2013, NMV F210389 (1) (former registration SEA-3046; donated to Museum Victoria).

Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_107, WAM station no 1, barcode 10000001, from -15.514826 124.183111 46 m to -15.514503 124.183774 45 m, 14 Mar 2015, WAM Z89014 (1); RV *Solander*, sled, site no SOL_60, WAM station no 9, barcode 10000582, from -15.311436 124.162869 42 m to -15.311705 124.162473 42 m, 16 Mar 2015, WAM Z89015 (1); RV *Solander*, sled, site no SOL_60, WAM station no 9, barcode 10000647, from -15.311436 124.162869 42 m to -15.311705 124.162473 42 m, 16 Mar 2015, WAM Z89016 (1); RV *Solander*, sled, site no LIN_36, WAM station no 17, barcode 10001114, from -15.220444 124.320894 50 m to -15.220159 124.320648 50 m, 18 Mar 2015, WAM Z89017 (5); RV *Solander*, sled, site no SOL_32, WAM station no 19, barcode 10001331, from -15.253592 124.203038 45 m to -15.253318 124.202302 45 m, 19 Mar 2015, WAM Z89018 (6); RV *Solander*, sled, site no SOL_56, WAM station no 20, barcode 10001420, from -15.376537 124.192773 35 m to -15.376196 124.192071 35 m, 19 Mar 2015, WAM Z89019 (1); RV *Solander*, sled, site no SOL_84, WAM station no 21, barcode 10001560, from -15.414697 124.059193 36 m to -15.415001 124.059918 36 m, 20 Mar 2015, WAM Z89020 (1); RV *Solander*, sled, site no SOL_24, WAM station no 23, barcode 10001767, from -15.406428 124.125928 42 m to -15.406937 124.125369 42 m, 20 Mar 2015, WAM Z89021 (1); RV *Solander*, sled, site no SOL_160, WAM station no 25, barcode 10001971, from -15.428534 124.273164 17 m to -15.428908 124.273525 17 m, 21 Mar 2015, WAM Z89022 (2); RV *Solander*, sled, site no SOL_109a, WAM station no 33, barcode 10002500, from -15.711677 124.2303 25 m to -15.711054 124.229793 25 m, 23 Mar 2015, WAM Z89023 (1); RV *Solander*, sled, site no SOL_73, WAM station no 38, barcode 10002692, from -15.945442 124.366373 29 m to -15.945268 124.367171 28 m, 25 Mar 2015, WAM Z89024 (1); RV *Solander*, sled, site no SOL_69, WAM station no 41, barcode 10002871, from -15.747648 124.146502 43 m to -15.747285 124.14634 43 m, 26 Mar 2015, WAM Z89025 (1).

Joseph Bonaparte Gulf, cruise SOL 4934, station 33, sample 29024, -11.65 129.83 24 m, NMV F201791 (11) (tissue code MOL AF 1516); NMV F173258; NMV F173259; NMV F173260; NMV F173261; NMV F201781; NMV F201782; NMV F201788; NMV F201789; NMV F201790; NMV F201792; NMV F203004

Other Northern Australia, NMV F95253; NMV F95254; NMV F95255; NMV F95256; NMV F112191; NMV F112192; NMV F113573; NMV F113574; NMV F113575; NMV F113576; NMV F113577; NMV F113578; NMV F113579; NMV F113580; NMV F113581; NMV F149742.

Great Australian Bight, NMV F113582; NMV F199464.

Description. Body quadrangular in section, slightly tapered towards oral and anal ends, anal end slightly upturned, preserved body (excluding tentacles) up to 98 mm long, body surface with tessellated appearance or smooth; body and

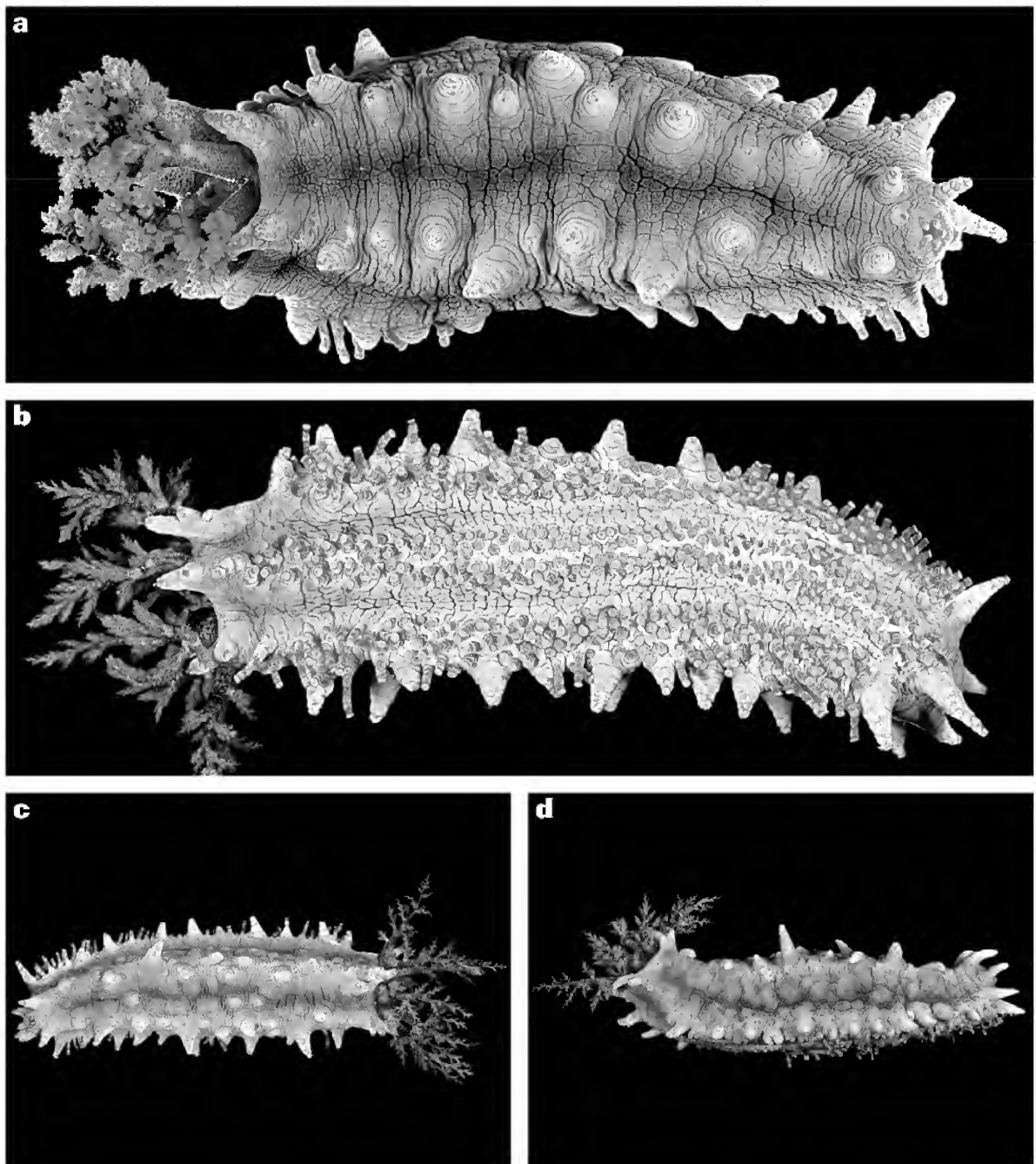


Figure 7. Photos of live specimens of *Colochirus quadrangularis* Troschel, 1846 from Singapore waters, provided by Helen Pei San Wong and Joo Yong Ong (TMSI of NUS; specimens estimated to be up to 60 mm long): a, dorsal view showing anal scales and absence of warts; b, ventral view; c, dorsal view showing warts; d, lateral view.

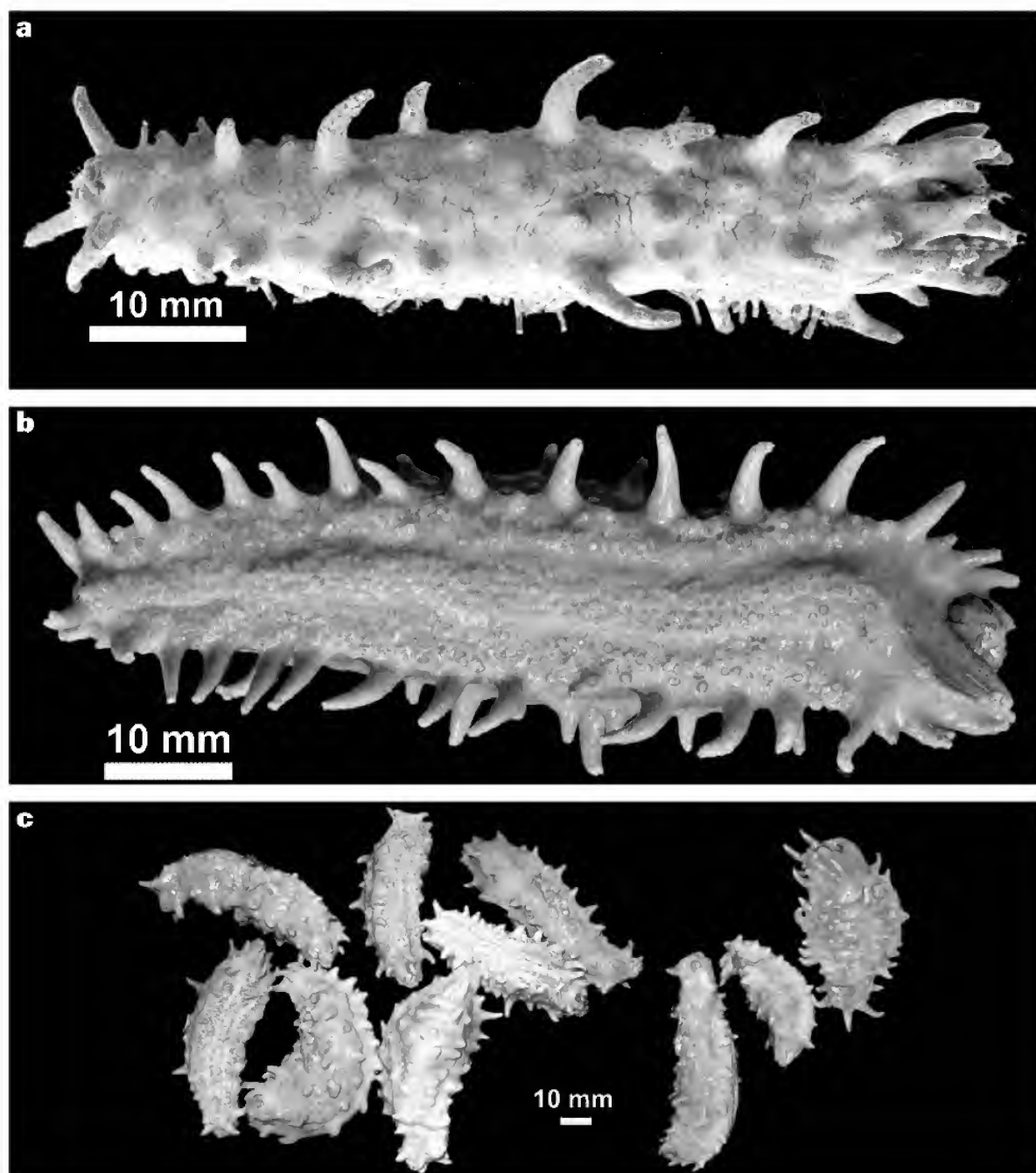


Figure 8. Photos of live specimens of *Colochirus quadrangularis* Troschel, 1846 from northern Australia: a, dorsal view (WAM Z89021, from Camden Sound); b, ventral view (WAM Z89015, from Camden Sound); c, colour morphs from Joseph Bonaparte Gulf (NMV F201791).

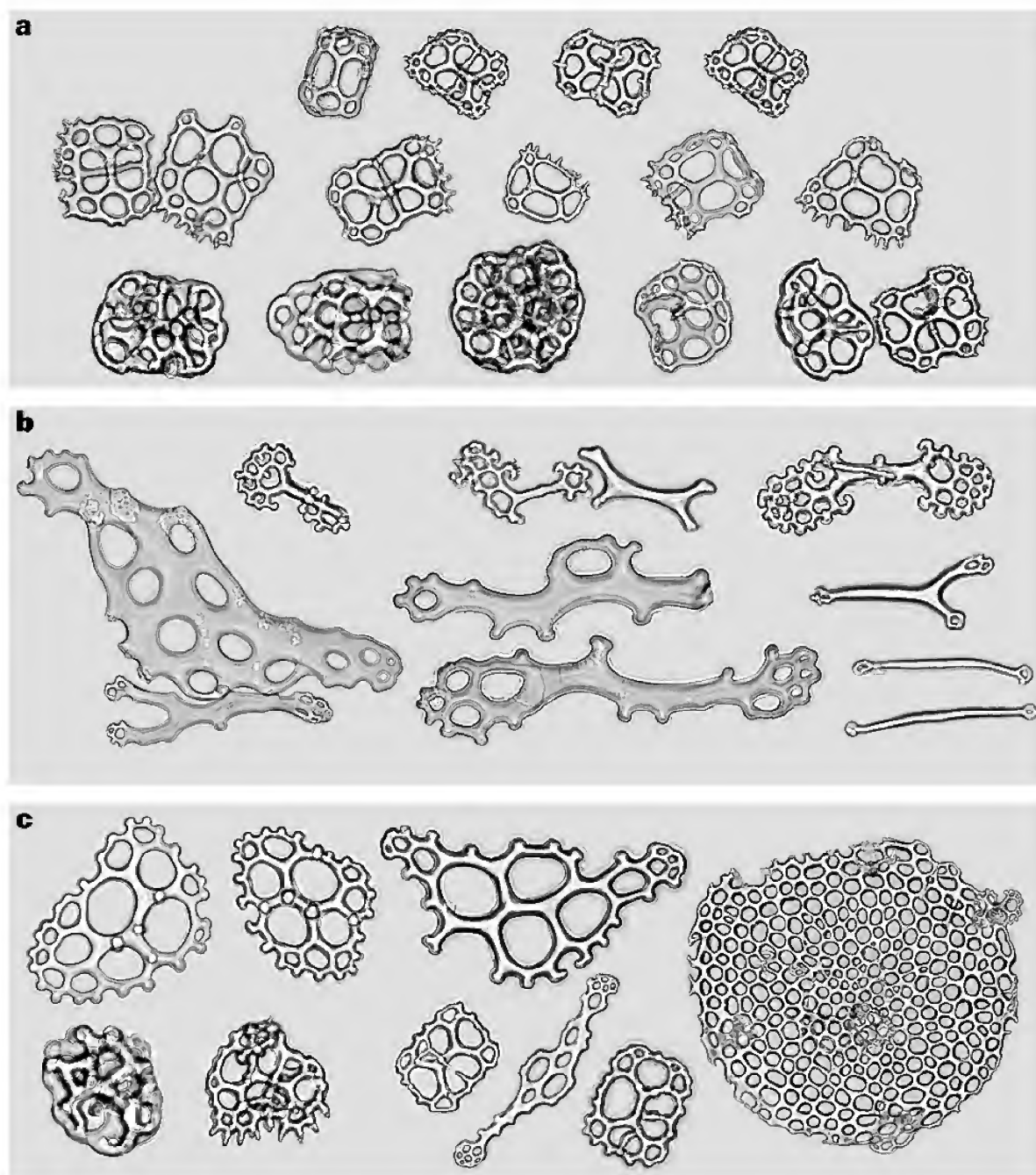


Figure 9. Ossicles from specimens of *Colochirus quadrangularis* Troschel, 1846 from Singapore: a, dorsal and peri-anal body wall bowls up to 56 μm long (three with single bridge) (top row), bowls with one spinous margin up to 80 μm long (three with single bridge) (middle row), hollow ellipsoids up to 88 μm long, and ellipsoids with inner bridges up to 88 μm long (bottom row) (from Singapore specimen NMV F210388); b, tentacle rods and rod-plates up to 440 μm long, rosettes up to 96 μm long (from NMV F210388); c, ventral tube foot endplate up to 400 μm diameter (right), support rod-plates up to 272 μm long, small bowls, spinous-edge bowl with bridging, and ellipsoid with internal bridging (bottom left) (from NMV F210389).

papillae firm, densely packed with ossicles; dorsal and ventro-lateral radii slightly raised, each with about 12 conical papillae in irregular zig-zag rows, papilla lengths variable up to about 10 mm long, papillae variably straight to curved, surmounted by tube feet ventro-laterally and sometimes dorsally, anterior and posterior ventral radii all with papillae; dorsal and lateral inter-radii slightly depressed, variably with or lacking scattered short conical or wart-like protuberances, lacking tube feet; 5 anterior oral valves, each with a terminal papilla and sometimes 1 or 2 additional papillae; 5 inner anal scales, some small peri-anal papillae, 5 longer proximal anal radial papillae; 10 dendritic tentacles, ventral 2 smaller; calcareous ring plates not forked posteriorly and lacking posterior prolongations; tube feet in discrete bands on ventral radii, each band about 4 wide, discrete inter-radii usually lacking tube feet, ventral inter-radii similar in width to the radial bands of tube feet.

Intergrading ossicle forms of dorsal mid-body wall (from NMV F210388):

1. on body wall surface, irregular oval to rounded-rectangular shallow bowls, long margins sometimes indented, four large central perforations, usually four small corner perforations, sometimes additional smaller marginal perforations, rim variably smooth or with fine knobs or fine blunt spines, bowls with or lacking bridges across rim, bowls up to rarely 56 μm long;
2. outer body wall, abundant rounded-rectangular to oval to irregular shallow bowls, four large central perforations, smaller peripheral perforations, one short or long margin prominently spinous, bowls variably partly bridged or not, up to 80 μm long;
3. inner body wall, some rounded-rectangular to oval shallow bowls, 4 large central perforations, smaller peripheral perforations, margin smooth, up to 96 μm long, sometimes partly bridged;
4. inner body wall, shallow bowls bridged on one side to create smooth, hollow irregular ellipsoids, up to 88 μm long;
5. inner body wall, shallow bowls, frequently thick-walled, bridged to create an upper surface and hollow ellipsoid, and inner-bridged irregular ellipsoids, not hollow, typically up to 88 μm long, rarely up to 136 μm long, some becoming enlarged and inter-grading with multi-layered scales;
6. underlying, multi-layered plates (scales), irregularly round to oval, up to at least 1.6 mm across/long.

Tentacle ossicles (from NMV F210388) elongate, thick, smooth, perforated rod-plates, curved and bent, up to 440 μm long; fine distally perforate rods; rosettes, up to 96 μm long.

Tube feet ossicles (from NMV F210389) endplates, uniform slightly irregular perforations, 400 μm diameter; endplate support rod-plates, narrow to elongate oval, to rounded triangular, smooth or knobbed, curved and bent, up to 272 μm long; spinous-edge bowls, variably bridged, as in dorsal body wall; shallow small bowls, variably knobbed, as in dorsal body wall; shallow larger bowls, margin and surface knobbed, two large and two smaller central perforations, smaller peripheral perforations, up to 88 μm long; hollow and inner-layered irregular ellipsoids as in dorsal body wall.

Live colour: radii and papillae variably red; dorsal and lateral inter-radii variably greenish; ventral inter-radii pale green; dendritic tentacles ends red; tentacle trunks greenish yellow with dark brown to black flecking; ventral tube feet red. Preserved colour: pale to dark grey.

Distribution. Through the tropical Indo-West-Pacific, from Zanzibar to Malaysia and Australia; 0–115 m (depth from Rowe & Gates 1995).

Remarks. We have observed specimens from Singapore waters that we judge to be *Colochirus quadrangularis*. Because of the proximal continuity of Singapore waters with those of the Straits of Malacca, we judge that the Singapore specimens are conspecific with those of the type locality. The live colour photos of *Colochirus quadrangularis* from Singapore waters that we have included here were provided for our work by our colleagues Wong Pei San Helen and Joo Yong Ong (NUS TMSI). The specimens studied here were donated to Museum Victoria by the Lee Kong Chian Natural History Museum in Singapore, the donation facilitated by our colleagues Wong Pei San Helen and Joo Yong Ong. The description above incorporates observations by these colleagues of 139 specimens of this species in the Lee Kong Chian Natural History Museum.

The conspicuous and distinctive ossicle form in the upper body wall of *Colochirus quadrangularis* is the irregular shallow sub-rectangular bowl with one strongly spinous edge.

Leptopentacta grisea H. L. Clark, 1938

Table 1; appendix 1; figure 10a

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Linnaeus*, sled, site no LIN_50, barcode 53713, from -15.37072 124.69674 9 m to -15.36572 124.6978 9 m, 16 Mar 2015, WAM Z89027.

Plesiocolochirus Cherbonnier, 1946

Figure 1; appendices 1, 2

Acolochirus H. L. Clark, 1946: 395.—Panning, 1971: 41 (synonymy by Rowe in Rowe & Gates 1995)

Apentacta H. L. Clark, 1946: 395 (synonymy by Panning 1971, and Clark & Rowe 1971)

Plesiocolochirus Cherbonnier, 1946: 286.—Panning, 1949: 448–449.—Panning, 1971: 42.—Rowe (in Rowe & Gates), 1995: 277.

Type species. *Plesiocolochirus spinosus* (Quoy & Gaimard, 1834) (original designation)

Type species locality. Eastern Australia, New South Wales, Port Jackson.

Other assigned species (with type locality added). *Plesiocolochirus armatus* (Marenzeller von, 1881) (China); *P. australis* (Ludwig, 1875) (NE Australia, Bowen); *P. challengerii* (Théel, 1886) (N Australia, Torres Strait); *P. dispar* (Lampert, 1889) (NW Australia, Mermaid Strait); *P. ignavus* (Ludwig, 1875) (S Australia, Gulf St Vincent); *P. inornatus* (Marenzeller von, 1881) (China); *P. minaeus* sp. nov. (NW Australia, Camden Sound, below); *P. minutus* (Ludwig, 1875) (NE Australia, Bowen); *P. tessellarius* (Cherbonnier, 1970) (Mozambique Channel).

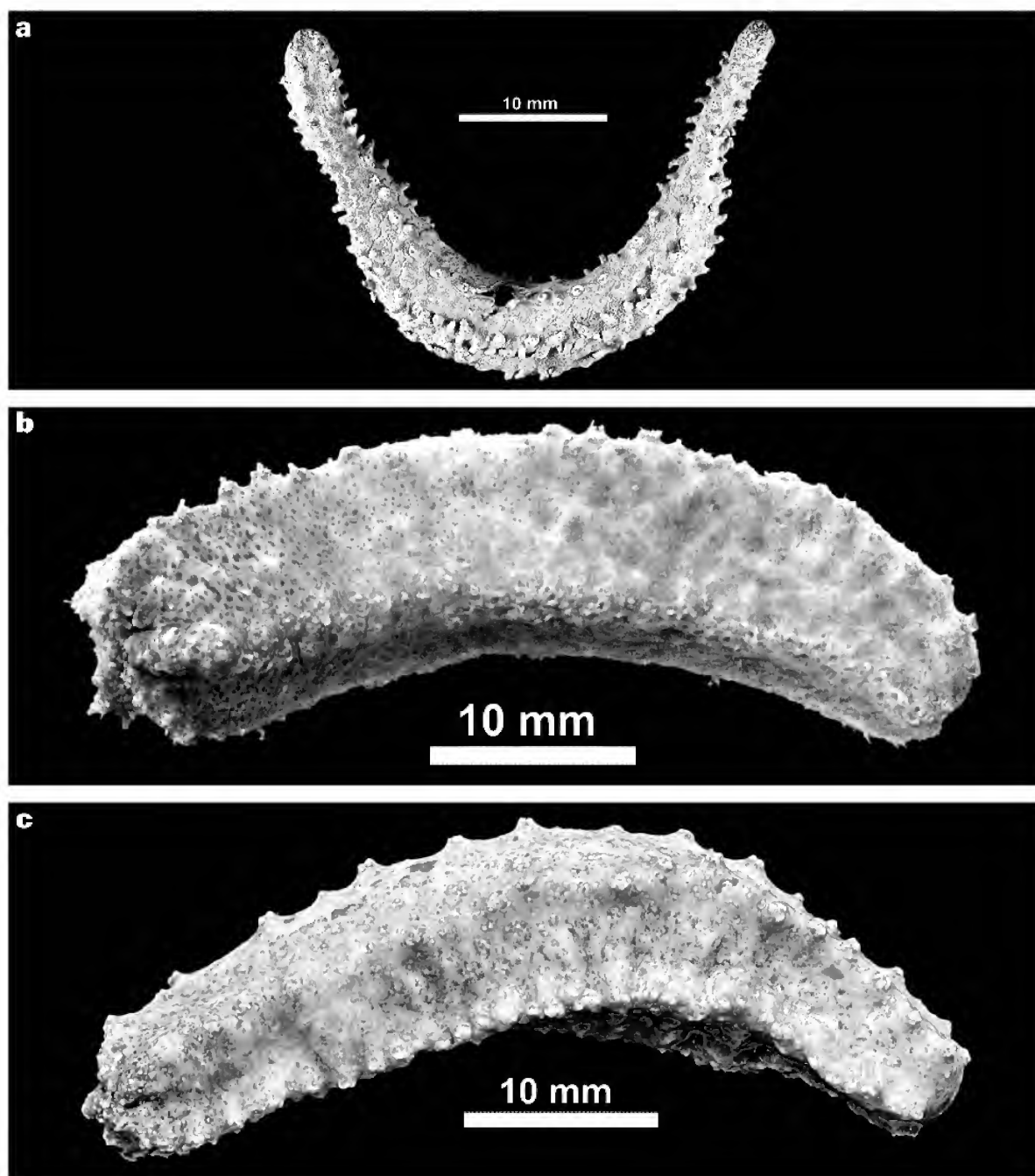


Figure 10. a, photo of lateral view of preserved specimen of *Leptopentacta grisea* H. L. Clark, 1938 (WAM Z89027). b, c, photos of live specimens of *Plesiocolochirus* species 1: b, dorsal view (WAM Z89028); c, lateral view (WAM Z89030).

Diagnosis (sensu stricto, based on type species only, described below). Body firm, packed with calcareous ossicles, fusiform with upturned oral and anal ends, long posterior taper, body oval in mid-body section, axial (not curved) length up to 64 mm; lateral edges of body with prominent, firm, conical papillae with imbricating scales; five conical oral valves, with imbricating scales distally; anal cone with large imbricating scales distally, large non-imbricating scales anterior to imbricating ones; small anal scales; small ossicles clustered into contiguous lumps in mid-body to create pseudo-scales, each with central passage/perforation for withdrawn tube feet, pseudo-scales about 1.00 mm across. Ten dendritic tentacles, 8 large, 2 small. Calcareous ring cucumariid-like, plates solid, higher than broad, lacking posterior prolongations. Tube feet scattered irregularly over body, inconspicuous, small, appear to penetrate pseudo-scales, more numerous ventrally than dorsally, mid-ventral radius with irregular paired rows, narrow space on each side of mid-ventral radius lacking tube feet.

Three intergrading ossicle forms of body wall:

1. surface layer of finely knobbed, shallow bowls, variably bridged across margins to sometimes create hollow, irregular, ellipsoid-like ossicles;
2. layer of flat, thickly knobbed buttons, some developing secondary layers to become small scales;
3. deeper layer of multi-layered scales.

Lateral papillae and tube feet with terminal endplates. Tentacle ossicles rods; lacking rosettes.

Remarks. Cherbonnier (1946) proposed that the following species be assigned to his new genus *Plesiocolochirus*: *Colochirus challengerii* Théel, 1886; *Colochirus gazellae* Lampert, 1889 (subsequently referred to *Loisettea* Rowe & Pawson, 1985); *Colochirus inornatus* von Marenzeller, 1881; *Thyone papillata* Sluiter, 1887 (subsequently referred to *Stolus* Selenka, 1867); *Colochirus squamatus* Sluiter, 1901 (subsequently synonymised with *Colochirus robustus* Östergren, 1898 by Rowe in Rowe & Gates 1995). Subsequently other species have been assigned to *Plesiocolochirus*: *Colochirus armatus* Marenzeller von, 1881 (China); *Colochirus australis* Ludwig, 1875 (NE Australia, Bowen); *Colochirus dispar* Lampert, 1889 (NW Australia, Mermaid Strait); *Cucumaria ignava* Ludwig, 1875 (S Australia, Gulf St Vincent); *Plesiocolochirus minaeus* sp. nov. (NW Australia, Camden Sound, below); *Colochirus minutus* Ludwig, 1875 (NE Australia, Bowen); *Pentacta tessellata* Cherbonnier, 1970 (Mozambique Channel).

Rowe (in Rowe & Gates) 1995 referred *Ocnus occiduus* O'Loughlin & O'Hara, 1992 to *Plesiocolochirus*, with reservations. This species was subsequently referred to *Australocnus* O'Loughlin & Alcock, 2000. In the same work Rowe judged that *Colochirus minutus* is a junior synonym of *Plesiocolochirus australis*. We provisionally raise *Colochirus minutus* out of synonymy for further consideration.

Phylogenetic data based on COI sequences (Figure 1) recover a clade of six species that appear to correspond to

Plesiocolochirus: *P. challengerii* (N Australia); *P. ignavus* (SE Australia); *P. minaeus* sp. nov. (below) (NW Australia); *P. tessellatus* (Comoros); *Plesiocolochirus* species 1 from NW Australia and Palau; *Plesiocolochirus* species 2 from NE Australia. The two unassigned species are close to specimens that have frequently been referred to *Plesiocolochirus australis* and *Plesiocolochirus minutus*, as well as to *Colochirus* sp. 1 mentioned above. A detailed study of these species, including study of relevant type specimens, is needed to determine the identity of these species and morphological boundaries of the *Colochirus* – *Plesiocolochirus* complex.

Unfortunately genetic data are not currently available for *Plesiocolochirus spinosus*, the type species of the genus. Morphologically this species is close to *Plesiocolochirus challengerii*. We anticipate from morphological observations that *Plesiocolochirus spinosus*, *Plesiocolochirus challengerii*, *Loisettea amphictena* Rowe & Pawson, 1985 and *Loisettea gazellae* will fall together in a clade distinct from the remaining species assigned to *Plesiocolochirus*.

Plesiocolochirus Cherbonnier, 1946 (based on type species *Plesiocolochirus spinosus* (Quoy & Gaimard, 1834), below) is distinguished *sensu stricto* from *Colochirus* Troschel, 1846 (based on type species *Colochirus quadrangularis* Troschel, 1846, above) by the following characters:

1. presence of large imbricating scales on distal anal cone, on proximal oral valves, and on lateral papillae;
2. presence of numerous inter-radial tube feet;
3. presence of knobbed button body wall ossicles;
4. absence of tentacle rosette ossicles.

Determination of the morphological limits of the clades corresponding to these genera awaits further study.

Plesiocolochirus spinosus (Quoy & Gaimard, 1834)

Figures 11, 12

Holothuria spinosa Quoy & Gaimard, 1834: 118–120, pl. 7 figs 1–10.

Cladolabes spinosus.— Brandt, 1835: 74.

Stolus firmus Selenka, 1867: 356, pl. 20 figs 118–119.

Ocnus spinosus.—Semper, 1867: 55.

Colochirus spinosus.—Selenka, 1868: 117.—von Marenzeller, 1881: 129–132.—Théel, 1886.—Lampert, 1889: 825–826.

Thyone spinosa.—Semper, 1869: 238.—Lampert, 1885: 157.

Stereoderma validum Bell, 1884: 150–151, pl. 9 figs Ea–f. (synonymy by H. L. Clark 1946)

Apentacta spinosa.—H. L. Clark, 1946: 395.

Plesiocolochirus spinosus.—Cherbonnier, 1946: 280–286, fig.—Rowe (in Rowe & Gates), 1995: 279.

Type locality. Australia, New South Wales, Port Jackson.

Material examined. S Queensland, Kimbla K4/69, -26.05 153.75 68 m, 1969, NMV F204081 (3); off Yeppoon, -24.05 151.45 9–37 m, 6 Sep 1967, NMV F204080 (1); off Yeppoon, Keppel Bay, -23.07 150.89 9 m, 6 Sep 1967, NMV F95257 (1).

Description. Body firm, packed with calcareous ossicles, fusiform with upturned oral and anal ends, long posterior taper,

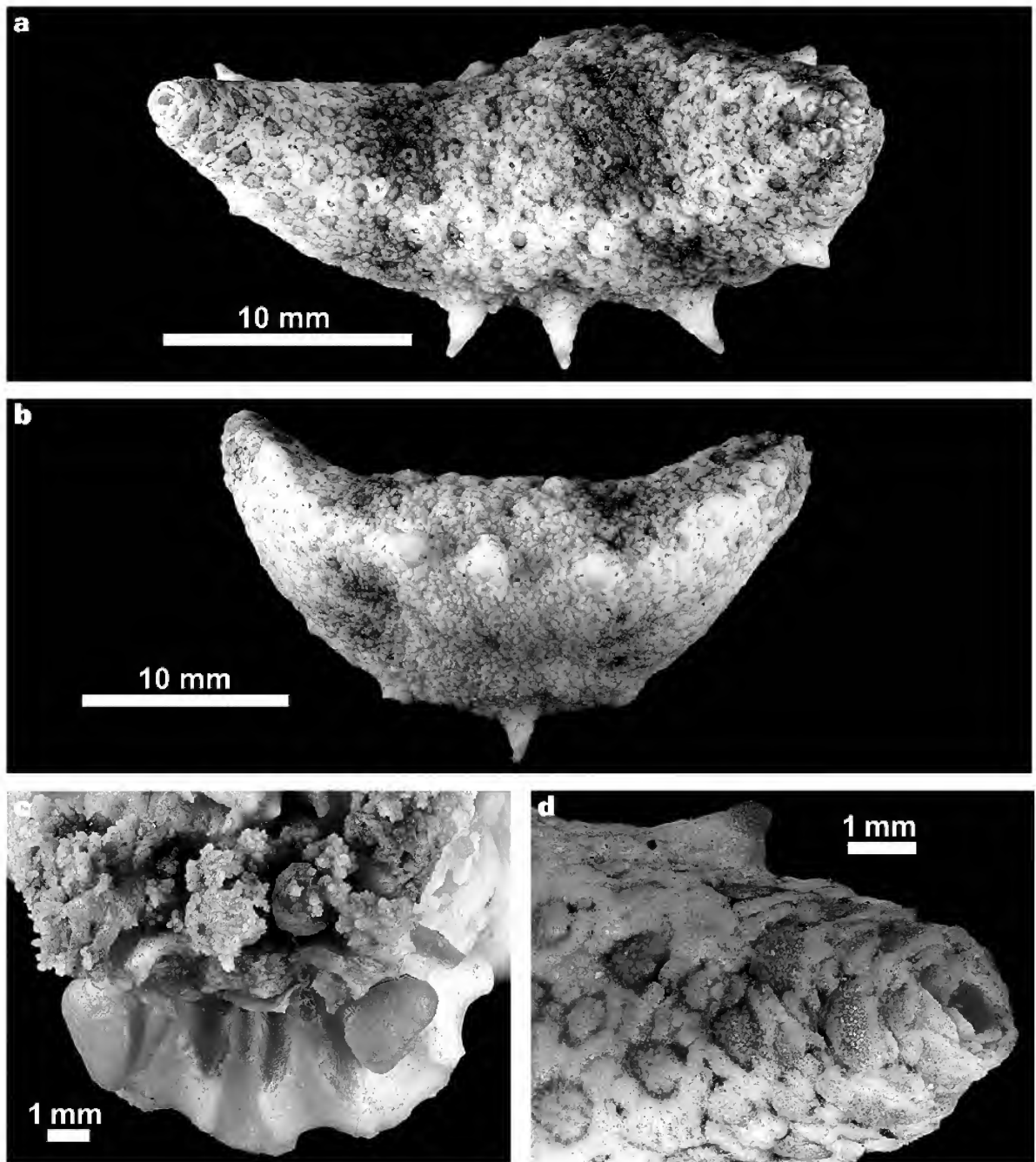


Figure 11. Photos of preserved specimen of *Plesiocolochirus spinosus* (Quoy & Gaimard, 1834) (NMV F204081): a, dorso-lateral view; b, ventro-lateral view; c, inter-radial and radial plates of the calcareous ring; d, peri-anal view with imbricating scales.

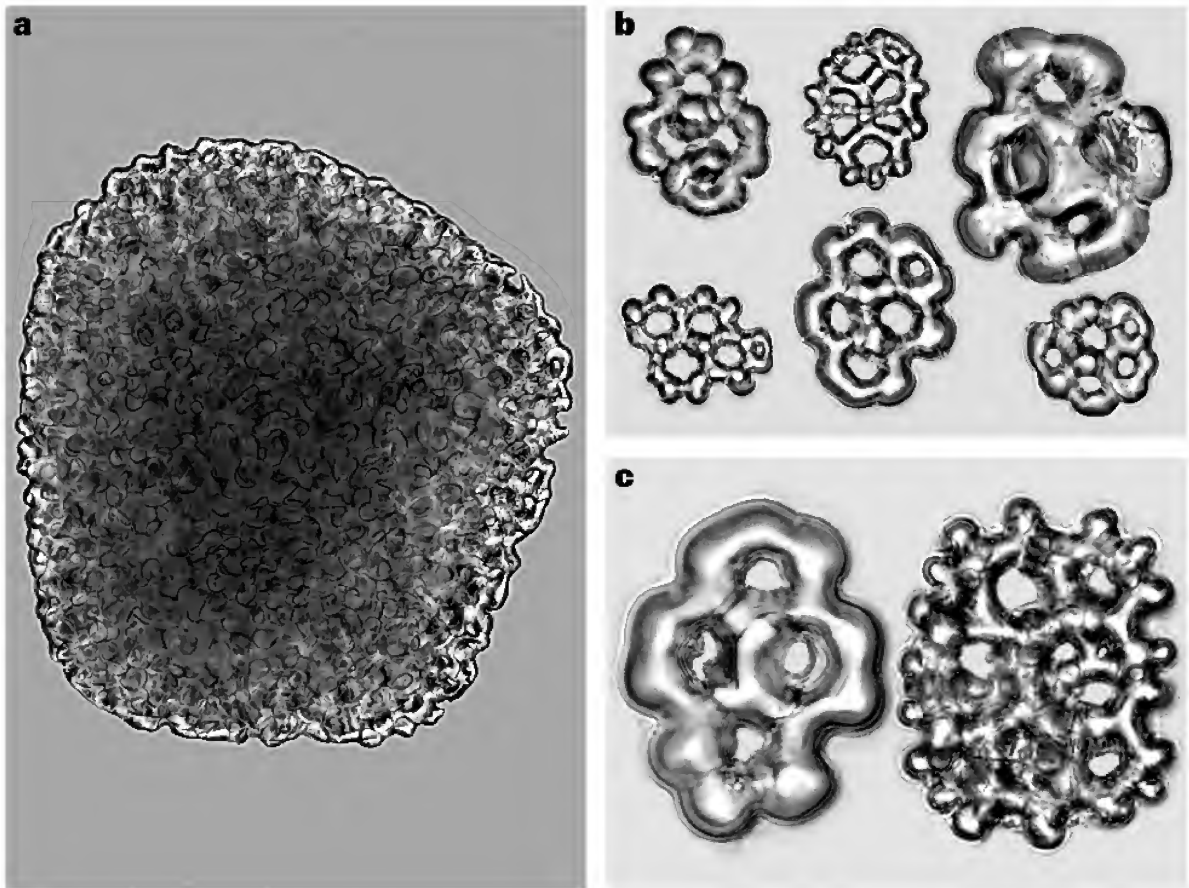


Figure 12. Ossicles from specimen of *Plesiocolochirus spinosus* (Quoy & Gaimard, 1834) (NMV F204081): a, multi-layered scale ossicle from body wall, up to 1.5 mm long; b, body wall thick buttons, up to 120 μm long, and fine knobbed bowls with (top center) and without (bottom left) a bridge, up to 70 μm long; c, body wall bridged ellipsoid-like bowl (right), up to 70 μm long, and thick button (left).

body oval in mid-body section, dorsal length shorter than ventral length, axial (not curved) length up to 64 mm; lateral edges of body with 3–12 firm conical papillae with large imbricating true scales, longest papillae mid-body, up to 6 mm long; five conical oral valves, each with two prominent spines distally, imbricating true scales distally; distal anal cone with large imbricating true scales, interspersed with small ossicle clumps; small anal scales; small ossicles clustered into contiguous lumps in mid-body to create pseudo-scales, each with central passage/perforation for withdrawn tube feet, pseudo-scales about 1.00 mm across. Ten dendritic tentacles, 8 large, 2 small. Calcareous ring cucumariid-like, plates solid, higher than broad, lacking posterior prolongations. Tube feet scattered irregularly over body, frequently withdrawn and inconspicuous, small, more numerous ventrally than dorsally, mid-ventral radius with irregular paired rows, narrow space on each side of mid-ventral radius lacking tube feet, tube feet appear to penetrate pseudo-scales.

Three inter-grading ossicle forms of body wall:

1. surface layer of finely knobbed bowls, oval to rounded rectangular in form, shallow concave, 4 central perforations, variable number of additional corner perforations, finely knobbed over surface, variably bridged from margins to sometimes create hollow, irregular, ellipsoid-like ossicles, 40–70 μm long;
2. layer of thickly knobbed buttons, flat, large marginal and central knobs, frequently 4 perforations but varying from 3–8, buttons 50–120 μm long, some buttons developing secondary layers to become small scales, up to about 216 μm long;
3. deeper layer of multi-layered scales, up to 1.5 mm long, developed from additional layers on knobbed plates.

Lateral papillae and tube feet with terminal endplates, fairly uniform perforations, about 120 μm .

Tentacle ossicles rods, lacking rosettes: large rods/rod-plates thick, curved, bent, perforated along rod, variable form, up to

480 μm long; small, irregularly-branched rods, some H-shaped, some distally perforate; fine very small distally perforate rods, not branched.

Live colour (Cherbonnier 1946, based on Quoy & Gaimard 1834): red dorsally, grey ventrally, lateral spines purple, tentacles red with brown spots at the base of the trunks. Preserved colour (this work): off-white to pale brown with some residual red flecks, two broad irregular transverse dark brown bands around mid-body.

Distribution (Rowe & Gates 1995). Eastern Australia, Queensland to Victoria, 9–90 m.

***Plesiocolochirus* species 1 (unresolved species complex)**

Table 1; appendices 1, 2; figures 1, 10b, c

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_4, WAM station no 22, barcode 10001662, from -15.446441 124.083021 62 m to -15.445955 124.083173 62 m, 20 Mar 2015, WAM Z89028 (1); RV *Solander*, sled, site no SOL_24, WAM station no 23, barcode 10001822, from -15.406428 124.125928 42 m to -15.406937 124.125369 42 m, 20 Mar 2015, WAM Z89029 (1); RV *Solander*, sled, site no SOL_43, WAM station no 26, barcode 10002101, from -15.488461 124.201824 46 m to -15.488309 124.201113 46 m, 21 Mar 2015, WAM Z89030 (1).

Remarks. We remarked under genus *Plesiocolochirus* (above) that the phylogenetic tree (Figure 1) supports two discrete and geographically separate *Plesiocolochirus* species clades from NE Australia (*Plesiocolochirus* species 2) and NW Australia (*Plesiocolochirus* species 1). Either clade might be representative of *Plesiocolochirus australis* or *Plesiocolochirus minutus*. Identification of the Camden species awaits morphological examination of the relevant types and additional phylogenetic data

***Plesiocolochirus minaeus* O’Loughlin sp. nov.**

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:189703BE-67E5-4212-B337-8C5B2F39D1E8>

Table 1; appendices 1, 2; figures 1, 13, 14;

Material examined. Holotype. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL 117, WAM station no 31, barcode 10002268, from -15.674833 124.279779 39 m to -15.674794 124.279012 39 m, 22 Mar 2015, WAM Z89026.

Description (preserved in 95% ethanol). Body hard, packed with calcareous ossicles, elongate, square in transverse section, 70 mm long, 10 mm high and wide; surface of body wall creased, imbricating scales around tips of papillae only; five anterior oral valves, lobed terminal papillae on each valve; each dorso-lateral margin with about 15 spaced, zig-zag, pyramidal, hard papillae, up to 2 mm high; ventro-lateral margin lacking papillae, except for 2–3 smaller papillae on each of the three ventral oral radii, and one on each of the three ventral anal radii; five tongue-like, radial anal scales/teeth; five pyramidal, radial, anal papillae, not as high as dorso-lateral papillae; dorsal and lateral inter-radii with scales evident,

irregular form and size, up to about 1.5 mm long. Ventral surface flat with three broad, raised radii with lace-like network of oblong scales each about 1 mm long, tube feet mostly deeply retracted, ventro-lateral radial tube feet band about four wide, mid-ventral band about five wide. Typical cucumariid calcareous ring, undulating posteriorly, lacking posterior prolongations. Ten dendritic tentacles, two ventral smaller. Single polian vesicle, gonad tubules not branched.

Dorsal body wall and dorso-lateral papillae ossicles of six intergrading types:

1. surface layer of deep bowls with tapering rounded base and bluntly to sharply spinous or knobbed marginal rim, some bridged internally, bowls typically about 55 μm wide 48 μm deep;
2. thick and thin walled shallow bowls, irregularly rectangular, many with smooth rims, many with indented lateral rims, variably bridged to create irregular hollow ellipsoids, frequently 55 μm long, up to 144 μm long;
3. smooth, irregularly round to oval, hollow ellipsoids, up to 64 μm across;
4. some regular, four-holed, thickened, flat buttons, up to 72 μm long;
5. abundant knobbed and thickened irregular flat buttons, many with incipient secondary layering, inter-grading with small multi-layered scales, up to about 176 μm long;
6. multi-layered ossicles/scales, irregularly oval, up to at least 1.00 mm long.

Dorso-lateral papillae lacking apical tube feet and endplates.

Ventral tube feet ossicles of four forms (lacking multi-layered ossicles and buttons):

1. endplates with fairly uniform perforations, smallest centrally, endplates up to at least 280 μm diameter;
2. straight and curved, smooth, tube foot support rod-plates, typically widened and perforated mid-rod and distally, some marginally denticulate, rod-plates up to 200 μm long;
3. knobbed oval to rectangular shallow bowls, margins knobbed to bluntly spinous, variably bridged to create irregular hollow ellipsoids, bowls up to 55 μm long;
4. shallow bowls of variable size, not bridged, some with marginal and surface knobs, bowls up to 128 μm long.

Tentacle ossicles of four inter-grading forms:

1. thick, smooth, perforated rod-plates up to 440 μm long;
2. smooth rods, variably perforated and branched
3. fine thin rods with distal perforations, typically about 60 μm long;
4. knobbed, branched rod rosettes, some perforated plates with knobbed margin, up to 50 μm long.

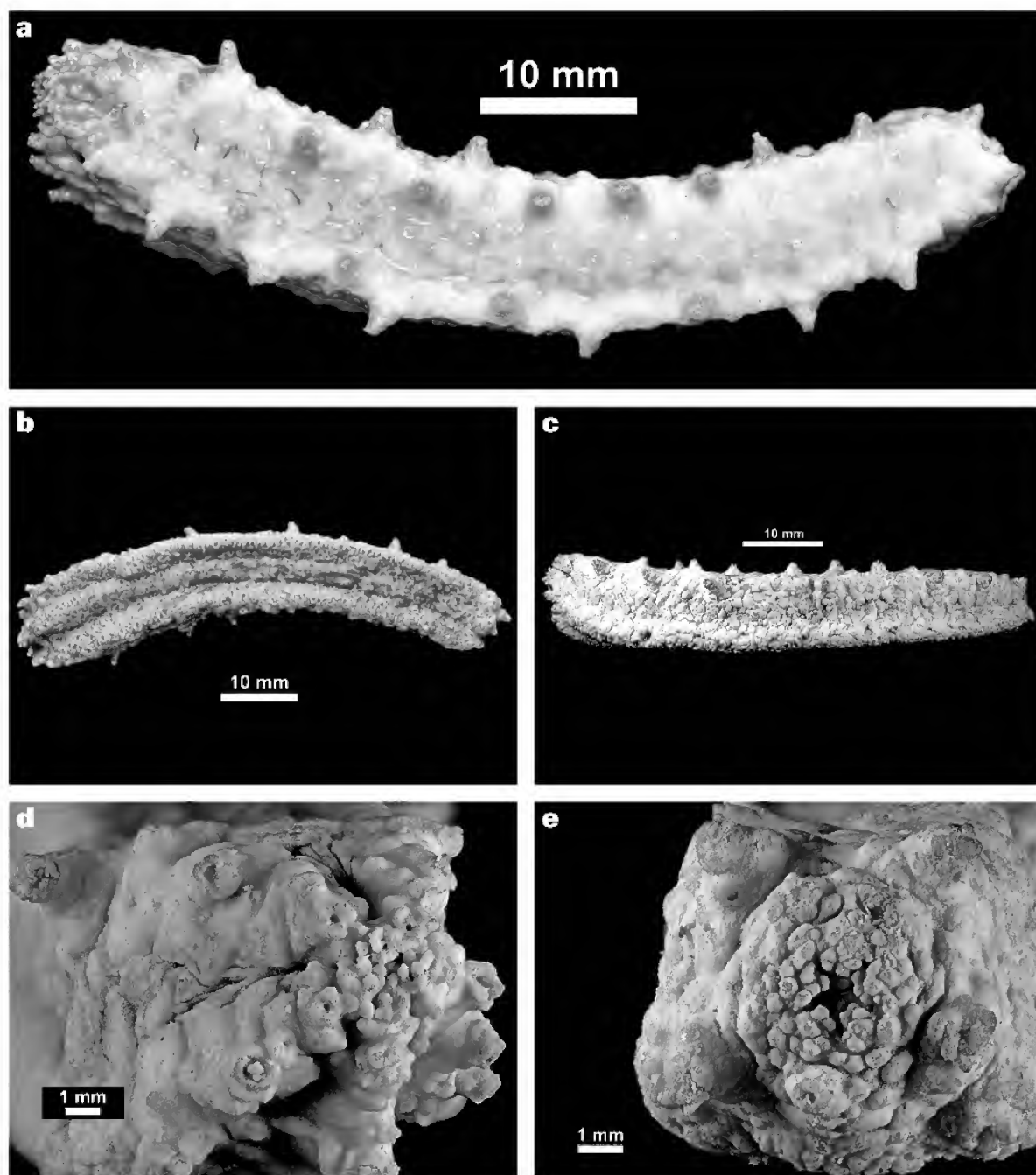


Figure 13. a, b, photos of live specimen of holotype of *Plesiocolochirus minaeus* O'Loughlin sp. nov. (WAM Z89026): a, dorsal view; b, ventral view. c–e, photos of preserved holotype: c, lateral view; d, oral view; e, anal view.

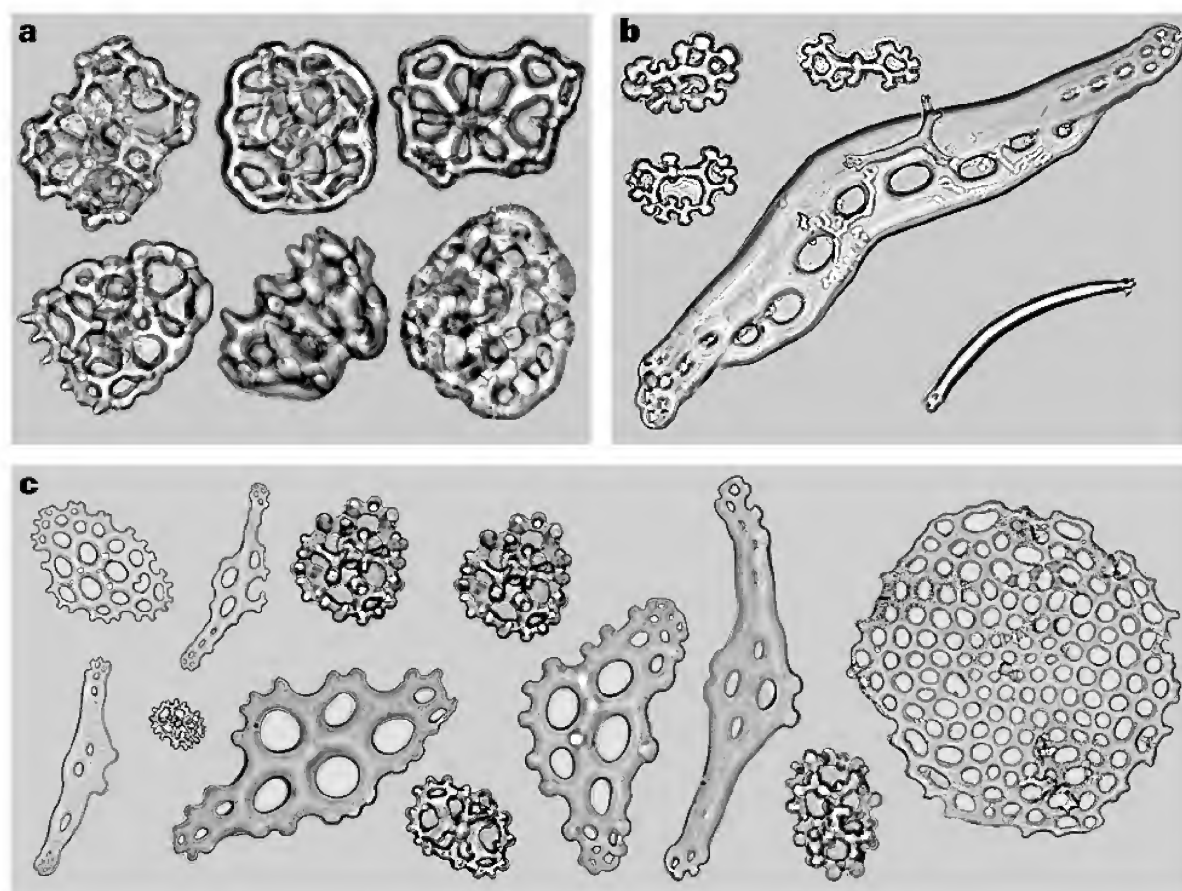


Figure 14. Ossicles from holotype of *Plesiocolochirus minaeus* O'Loughlin sp. nov. (WAM Z89026): a, dorsal body wall deep bowls with spinous rims about $55\ \mu\text{m}$ wide $48\ \mu\text{m}$ deep (bottom left and bottom center), shallow bowls variably bridged to create irregular hollow ellipsoids up to $144\ \mu\text{m}$ long (top row), knobbed button with secondary layering up to $176\ \mu\text{m}$ long (bottom right); b, tentacle fine rod and thick perforated rod up to $440\ \mu\text{m}$ long, rosettes up to $50\ \mu\text{m}$ long; c, ventral tube foot endplate up to at least $280\ \mu\text{m}$ long (right), support perforated rod-plates up to $200\ \mu\text{m}$ long, small shallow knobbed bowls variably bridged to create irregular hollow ellipsoids up to $55\ \mu\text{m}$ long, large shallow bowl not bridged up to $128\ \mu\text{m}$ long (top left).

Live body colour very pale yellow to off-white, dorso-lateral papillae and oral valves reddish-orange, ventral radii greenish yellow; preserved colour off-white.

Distribution. Northwest Western Australia, Kimberley Region, Camden Sound, 39 m.

Etymology. From the Latin *minae* ("parapets"), with reference to the parapet-like hard papillae on the dorso-lateral margins of the body in lateral view.

Remarks. The phylogenetic tree (Figure 1) includes a CO1 sequence for the new species, *Plesiocolochirus minaeus* O'Loughlin, within the congeneric clade of *Plesiocolochirus* species. This sequence is understandably remote from the *Plesiocolochirus challengerii* clade that we anticipate on morphological grounds will be a clade close to *Plesiocolochirus spinosus*.

The morphological characters that distinguish *Plesiocolochirus minaeus* O'Loughlin sp. nov. from other *Plesiocolochirus* species are the:

1. pyramidal, firm, dorso-lateral papillae;
2. complete absence of a ventro-lateral raised firm papillae;
3. absence of inter-radial tube feet;
4. presence of imbricating scales at tips of dorso-lateral papillae only;
5. abundance of knobbed and thickened irregular buttons in the body wall, many with incipient secondary layering, intergrading with small multi-layered scales;
6. ventral tube feet surrounded by a ring of about four ellipsoidal scales, not penetrating scales;

7. live colour of red dorso-lateral papillae on off-white body.

We note the presence of tentacle rosettes in the new species. This indicates that the presence or absence of tentacle rosettes is not a sound generic diagnostic character for genera *Colochirus* and *Plesiocolochirus*.

We also note the presence of two Pilumnidae crabs in the coelom of the holotype of the new species.

***Pseudocolochirus axiologus* (H. L. Clark, 1914)**

Table 1; appendix 1; figures 15, 16

Colochirus axiologus H. L. Clark, 1914: 171–173, pl. 25.—Ekman, 1918: 26–28, pl. 2 fig. 1, pl. 3 figs 16–19.

Pseudocolochirus axiologus (H. L. Clark, 1938): 456–457.—1946: 394.

Pseudocolochirus violaceus (Théel, 1886).—Cherbonnier, 1988: 174–177, figs 73, 74 (part; N Australia specimens are *P. axiologus*).—Rowe (in Rowe & Gates), 1995: 280 (part; N Australia specimens are *P. axiologus*).

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no LIN_35, WAM station no 23, barcode 10000760, from -15.363088 124.44389 37 m to -15.362756 124.443995 37 m, 17 Mar 2015, WAM Z89031 (1); RV *Solander*, sled, site no SOL_49, WAM station no 32, barcode 10002389, from -15.668951 124.357909 41 m to -15.669007 124.357529 42 m, 22 Mar 2015, WAM Z89032 (1).

WA, northwest shelf, -12.84 125.68 88–97 m, 2 Apr 1981, NMV F112187 (1); -12.90 125.58 84–88 m, 2 Feb 1981, NMV F112188 (2); -12.90 125.59 83 m, 2 Apr 1981, NMV F112189 (2); -12.83 125.7 91 m, 1 Apr 1981, NMV F112190 (1).

Northern Territory, Joseph Bonaparte Gulf, -11.54 129.82 60 m, 12 Sep 2009, NMV F202986 (1) (tissue code MOL AF 1512); -10.31 129.62 89 m, 1 Sep 2009, NMV F202987 (1) (tissue code MOL AF 1504); -11.01 129.79 55 m., 6 Sep 2009, NMV F202988 (2) (tissue code MOL AF 1507).

Queensland, Gulf of Carpentaria, -11.37 141.42 35 m, 9 Sep 1982, NMV F95259 (1) (tissue code MoV 4627).

Remarks. H. L. Clark (1914) noted the following features for the type of his *Colochirus axiologus*:

1. 90 mm axial (horizontal) length;
2. tube feet confined to ventral ambulacra;
3. absence of ossicles in the body wall;
4. bright purple colour around the tentacle aperture;
5. body colour purplish-rose.

When describing additional specimens, H. L. Clark (1938) referred his species to *Pseudocolochirus* Pearson, 1910, and confirmed the absence of tube feet other than on the ventral ambulacra, and the absence of ossicles in the body wall. H. L. Clark (1938) acknowledged that Ekman (1918) found and illustrated distinctive ossicles in the body wall of small specimens (41–49 mm long) of what he judged to be *Colochirus axiologus*, and Clark concluded that ossicles disappear with increase in size of specimens.

We examined a small specimen (40 mm axial preserved length) from Joseph Bonaparte Gulf (NMV F202988) that

lacked ossicles in the mid-body wall but did have a few almost inconspicuous tube feet on the dorsal anterior radii (that H. L. Clark 1938 had also noted on his specimens). We also found endplate support rod-plates in the ventral tube feet, and distinctive small thick plates in the nearby body wall with very small to no perforations. These ossicles were frequently dumbbell-shaped and lacked perforations, or had up to three very small ones. The plates varied in size from 40–90 μ m long. We found similar small plates near the ventral tube feet in a larger specimen (100 mm axial preserved length) from Camden Sound (WAM Z89032). These buttons were larger, up to 200 μ m long, and more irregular in form. There were a few anterior dorsal radial hard papillae in which we found multi-layered ossicles fragments, and large single-layered perforated plate fragments up to 440 μ m long.

We judge that the specimens examined by H. L. Clark (1914, 1938), Ekman (1918) and us are conspecific and belong to *Pseudocolochirus axiologus* (H. L. Clark, 1914). We acknowledge that this species is similar to *Pseudocolochirus violaceus* (Théel, 1886). We do not accept the synonymy of these two species by Cherbonnier (1988). *Pseudocolochirus violaceus* has the following differing characters:

1. the whole body, both radial and inter-radial, is covered with small papillae;
2. tube feet are clearly evident on the dorsal radii;
3. the distinctive plates are present in the mid-body wall;
4. prominent anterior and posterior papillae are more numerous.

We raise *Pseudocolochirus axiologus* (H. L. Clark, 1914) out of synonymy (by Cherbonnier 1988) with *Pseudocolochirus violaceus* (Théel, 1886). Rowe (in Rowe & Gates, 1995) followed Cherbonnier (1988) who considered all *Pseudocolochirus* species to be synonyms, with *Pseudocolochirus violaceus* the senior synonym. We judge that northern Australian specimens are *Pseudocolochirus axiologus*, not *P. violaceus* (see synonymy above).

Family **Phyllophoridae** Östergren, 1907 (*sensu* Pawson & Fell 1965)

***Phyllophorella spiculata* (Chang, 1935)**

Table 1; appendix 1; figure 17b

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_32, WAM station no 19, barcode 10001306, from -15.253592 124.203038 45 m to -15.253318 124.202302 45 m, 19 Mar 2015, WAM Z89033 (1).

Remarks. We note that O'Loughlin *et al.* (2012) raised *Phyllophorella* to generic status.

***Phyllophorus (Urodemella) holothurioides* Ludwig, 1875**

Table 1; appendix 1; figure 17a

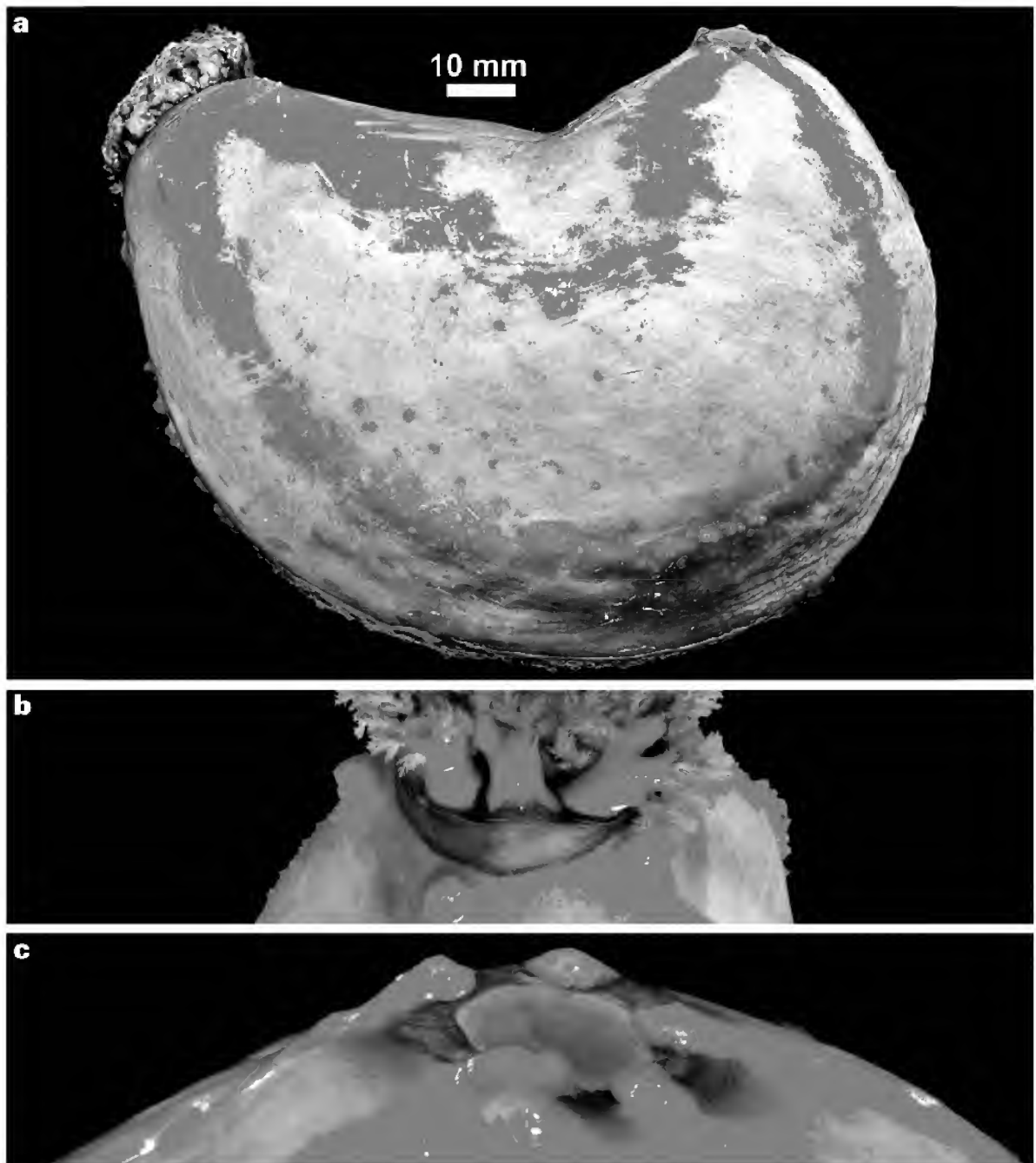


Figure 15. Photos of live specimen of *Pseudocolochirus axiologus* (H. L. Clark, 1914) (WAM Z89032): a, lateral view; b, peri-oral view; c, peri-anal view.

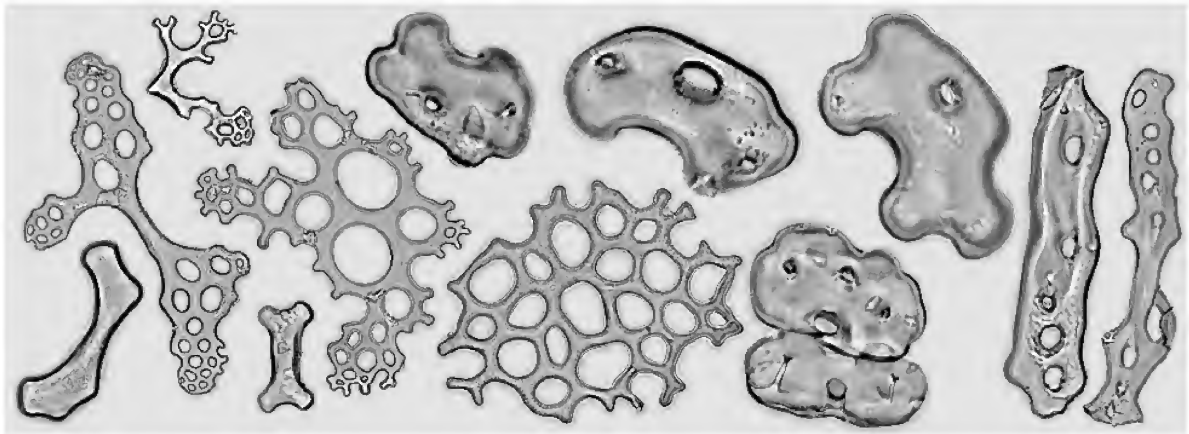


Figure 16. Ossicles from specimen of *Pseudocolochirus axiologus* (H. L. Clark, 1914) (WAM Z89031). From ventral tube feet and ventral body wall near tube feet: thick irregular oval to elongate plates with small perforations, plates up to 200 μm long; tube foot thick and thin support plates with distal small perforations, plates up to 256 μm long; small endplate (mid-lower).

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no LIN_46, WAM station no 3, barcode 10000113, from -15.399083 124.345337 41 m to -15.398828 124.345572 42 m, 15 Mar 2015, WAM Z89034 (1); RV *Solander*, sled, site no SOL_116a, WAM station no 18, barcode 10001277, from -15.261423 124.275183 41 m to -15.261716 124.275827 41 m, 18 Mar 2015, WAM Z89035 (1).

Family Sclerodactylidae Panning, 1949 (*sensu* Smirnov 2012)

Havelockia Pearson, 1903

Havelockia Pearson, 1903: 198.—Panning, 1949: 466, 468.—Rowe (in Rowe & Gates), 1995: 310.

Pentathylene Clark, H. L., 1938: 458–459.—1946: 386, 396.—Panning, 1949: 459.

Diagnosis (after Thandar 1989). Calcareous ring short, stout, only anterior projections of radial and inter-radial plates free; posterior paired process of radial plates divided into several pieces. Body wall ossicles tables with squarish to oval discs, usually perforated by four large central and four smaller peripheral perforations, that are sometimes reduced or absent; spire of two pillars joined at apex and terminating in a few blunt teeth.

Remarks. Thandar (1989) has discussed the above generic synonymy by Panning (1949), and the replacement of the type species *Havelockia herdmanni* Pearson, 1903 by the senior synonym *Havelockia versicolor* (Semper, 1867).

Havelockia versicolor (Semper, 1867)

Table 1; appendix 1; figures 18a–d

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_120, WAM station no 5, barcode 10000277, from -15.37669 124.248319 53 m to -15.377306 124.248179 53 m, 15 Mar 2015,

WAM Z89036 (1); RV *Solander*, sled, site no LIN_35, WAM station no 11, barcode 10000776, from -15.363088 124.44389 37 m to -15.362756 124.443995 37 m, 17 Mar 2015, WAM Z89037 (1); RV *Solander*, sled, site no LIN_6, WAM station no 16, barcode 10001220, from -15.27505 124.36988 46 m to -15.27543 124.369177 46 m, 18 Mar 2015, WAM Z89038 (1); RV *Solander*, sled, site no LIN_36, WAM station no 17, barcode 10001124, from -15.220444 124.320894 50 m to -15.220159 124.320648 50 m, 18 Mar 2015, WAM Z89039 (1); RV *Solander*, sled, site no SOL_32, WAM station no 19, barcode 10001321, from -15.253592 124.203038 45 m to -15.253318 124.202302 45 m, 19 Mar 2015, WAM Z89040 (1); RV *Solander*, sled, site no SOL_56, WAM station no 20, barcode 10001417, from -15.376537 124.192773 35 m to -15.376196 124.192071 35 m, 19 Mar 2015, WAM Z89041 (1); RV *Solander*, sled, site no SOL_4, WAM station no 22, barcode 10001637, from -15.446441 124.083021 62 m to -15.445944 124.083173 62 m, 20 Mar 2015, WAM Z89042 (1); RV *Solander*, sled, site no SOL_24, WAM station no 23, barcode 10001924, from -15.406428 124.125928 42 m to -15.406937 124.125369 42 m, 20 Mar 2015, WAM Z89043 (1); RV *Solander*, sled, site no SOL_49, WAM station no 32, barcode 10002314, from -15.668951 124.357909 41 m to -15.669007 124.357529 42 m, 22 Mar 2015, WAM Z89044 (1); RV *Solander*, sled, site no SOL_49, WAM station no 32, barcode 10002323, from -15.668951 124.357909 41 m to -15.669007 124.357529 42 m, 22 Mar 2015, WAM Z89045 (1); RV *Solander*, sled, site no SOL_73, WAM station no 38, barcode 10002688, from -15.945442 124.366373 29 m to -15.945268 124.367171 28 m, 25 Mar 2015, WAM Z89046 (1); RV *Solander*, sled, site no SOL_73, WAM station no 38, barcode 10002689, from -15.945442 124.366373 29 m to -15.945268 124.367171 28 m, 25 Mar 2015, WAM Z89047 (1); RV *Solander*, sled, site no SOL_97, WAM station no 39, barcode 10002752, from -15.782865 124.378047 32 m to -15.782335 124.378553 33 m, 25 Mar 2015, WAM Z89048 (1); RV *Solander*, sled, site no SOL_69, WAM station no 41, barcode 10002838, from -15.747648 124.146502 43 m to -15.747285 124.14634 43 m, 26 Mar 2015, WAM Z89049 (1); RV *Solander*, sled, site no SOL_47, WAM station no 42, barcode 10002939, from -15.612805 124.073033 36 m to -15.612437 124.072883 35 m, 26 Mar 2015, WAM Z89050 (1).

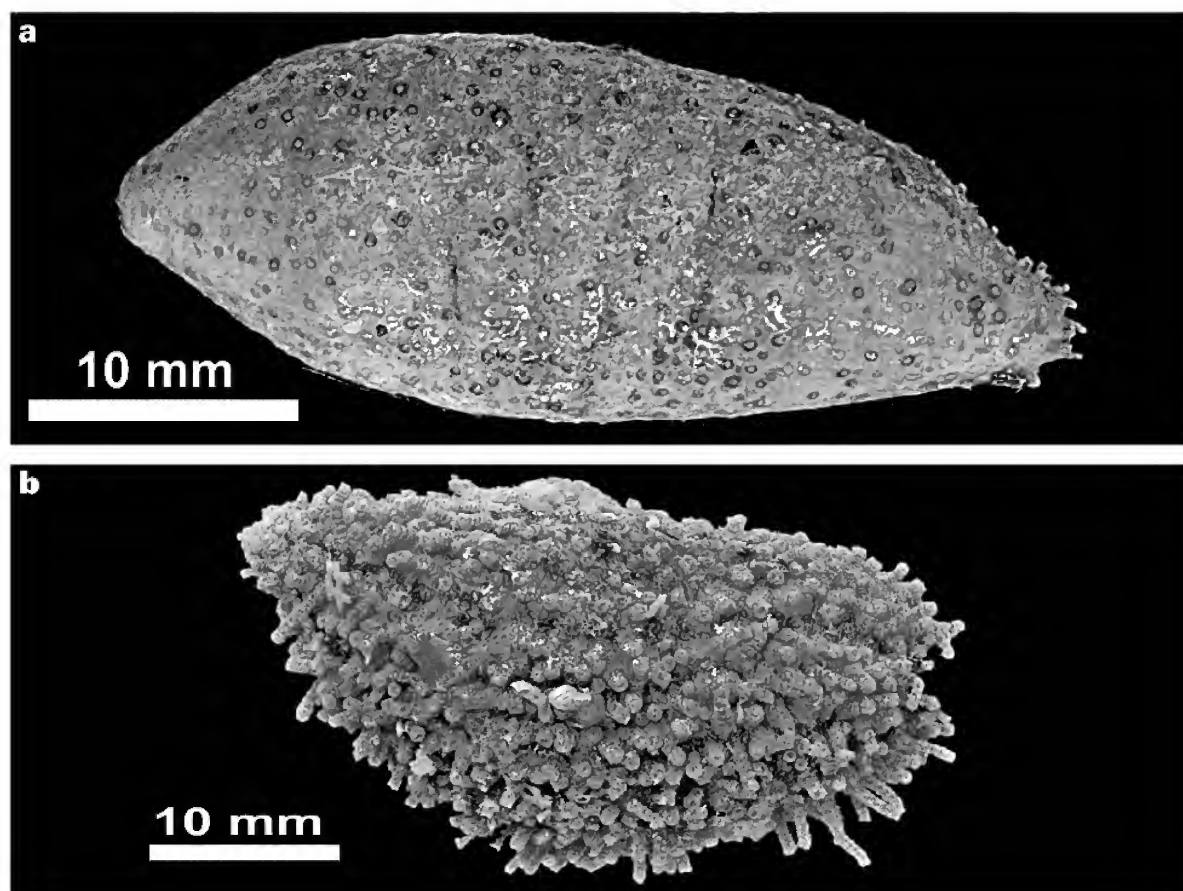


Figure 17. a, photo of dorsal view of live specimen of *Phyllophorus (Urodemella) holothuroides* Ludwig, 1875 (WAM Z89035). b, photo of lateral view of live specimen of *Phyllophorella spiculata* (Chang, 1835) (WAM Z89033).

Family **Thyonidae** Panning, 1949 (*sensu* Smirnov, 2012)

Subfamily **Semperiellinae** Heding & Panning, 1954

Diagnosis. See O'Loughlin, Mackenzie & VandenSpiegel 2014.

Remarks. See O'Loughlin, Mackenzie & VandenSpiegel 2014.

Massinium Samyn & Thandar, 2003

Massinium Samyn and Thandar, 2003: 136.—Samyn *et al.*, 2010: 2.—O'Loughlin *et al.*, 2012: 290.

Diagnosis (O'Loughlin, Mackenzie & VandenSpiegel 2014). Frequently semi-spherical species with oral and anal dorsal orientations; 20 dendritic tentacles arranged in two circles of 10 large outer and 10 small inner (proximal peri-oral); tube feet distributed all over mid-body; calcareous ring elongate, tubular, with both radial and inter-radial plates fragmented into a mosaic of small pieces, and posterior prolongations linked

distally to form inter-radial oval non-calcified spaces beneath the water vascular ring; polian vesicles from 1 to 4; ossicles variably include granuliform rods, rosettes, pseudo-buttons and tables; table spires with 1 or 2 or 3 or reduced pillars.

Remarks. See O'Loughlin, Mackenzie & VandenSpiegel 2014.

Massinium bonapartum O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel 2014)

Table 1; appendix 1; figure 19d

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_2, WAM station no 30, barcode 10002243, from -15.711306 124.315779 28 m to -15.71207 124.31566 28 m, 22 Mar 2015, WAM Z89051 (1); RV *Solander*, sled, site no SOL_73, WAM station no 38, barcode 10002725, from -15.945442 124.366373 29 m to -15.945268 124.367171 28 m, 25 Mar 2015, WAM Z89052 (1); RV *Solander*, sled, site no SOL_47, WAM station no 42, barcode 10002966, from -15.612805 124.073033 36 m to -15.612437 124.072883 35 m, 26 Mar 2015, WAM Z89053 (1).

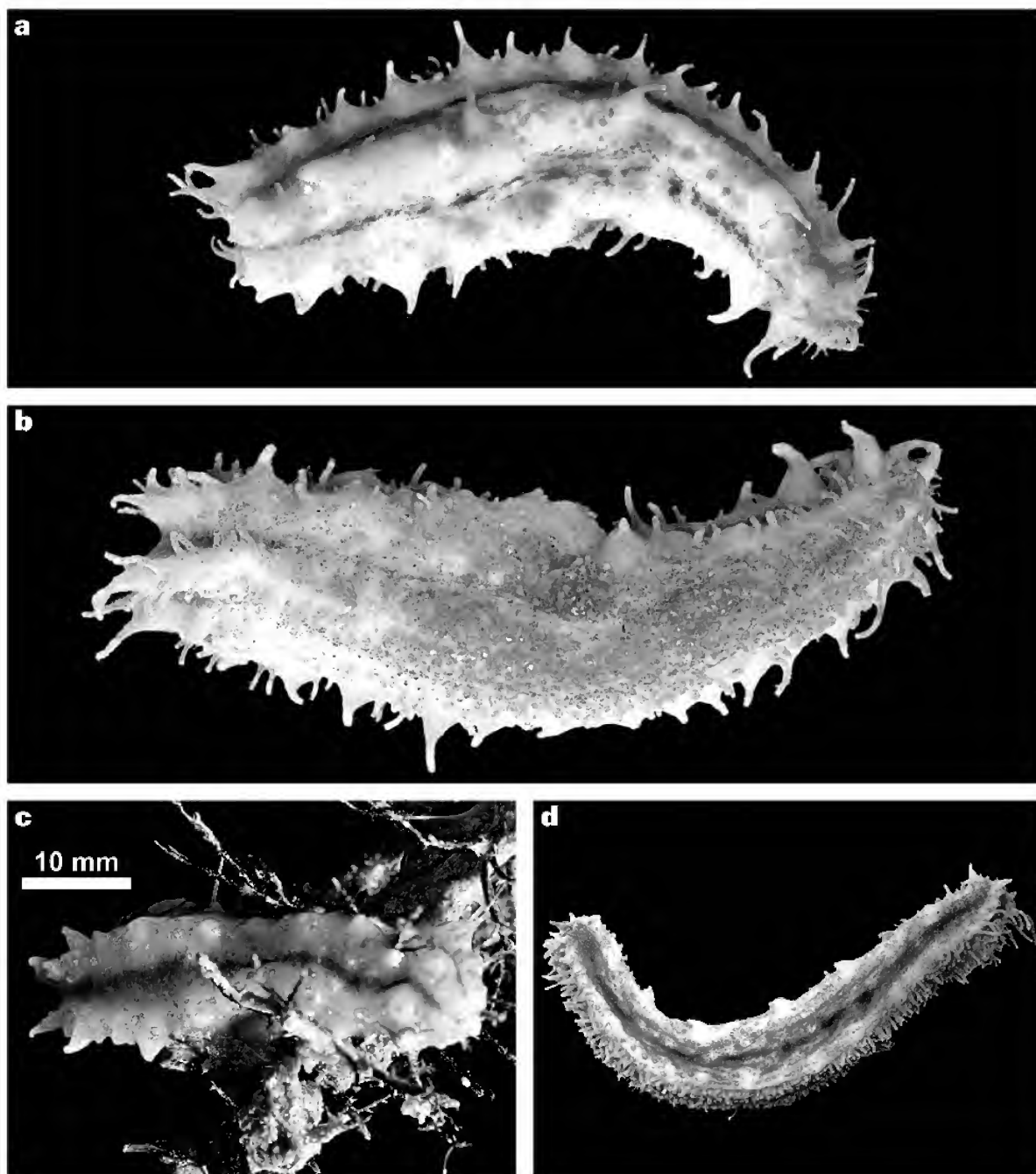


Figure 18. Photos of live specimens of *Havelockia versicolor* (Semper, 1867) (estimated 35–40 mm long live). a, dorsal view (WAM Z89047); b, ventral view (WAM Z89047); c, *in situ* view (WAM Z89043); d, lateral view (WAM Z89048).

Neothyonidium(?) insolitum O'Loughlin sp. nov.

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:7FCA7216-B862-4A4E-A829-07CA9DC0E23D>

Table 1; appendix 1; figures 19a–c, 20

Material examined. Holotype. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_47, WAM station no 42, barcode 10002958, from -15.612805 124.073033 36 m to -15.612437 124.072883 35 m, 26 Mar 2015, WAM Z89054.

Description. Body fusiform, cylindrical mid-body, tapered and rounded oral end, tapered anally to narrow end, live body variably 50 mm long, 13 mm diameter, body (preserved in 95% ethanol) 26 mm long, up to 14 mm diameter; complete cover of tube feet, more numerous ventrally than dorsally, tube feet diameters about 0.2 mm; tentacles in inner circle of five very small, outer circle of 13 large; calcareous ring elongate, tubular, with both radial and inter-radial plates fragmented into a mosaic of small pieces; inconspicuous anal scales detected; single polian vesicle.

Ossicles of mid-body wall numerous *Thyone*-like oval tables, discs with most frequently four perforations, sometimes with an additional four smaller corner perforations to create a rounded rectangular disc, discs up to 80 μ m long; spires two short pillars with one distal cross-bridge, two distal splayed spines at base of each pillar, spire height about 24 μ m. Tube feet endplates with variable diameters up to 224 μ m, irregular perforations and margin; rare tube foot support tables with elongate discs up to 80 μ m long; some tube foot support rods, similar to tentacle rods, sometimes forked distally with enlarged rounded ends with few small perforations. Peri-oral wall with tables similar to mid-body wall, but discs generally smaller, up to 55 μ m long. Peri-anal body wall with tables similar to mid-body wall, but smaller as in peri-oral region; small rosettes present; anal multi-layered scales present. Tentacles with thick and thin rods, distal ends swollen with small perforations; thick rods sometimes branched distally into widened ends with small perforations, thick rods up to 160 μ m long; thin rods up to 90 μ m long.

Live colour off-white to grey, semi-translucent; preserved colour off-white.

Distribution. Northwest Western Australia, Kimberley Region, Camden Sound, 35–36 m.

Etymology. From the Latin *insolitum* (meaning unusual), with reference to the unusual combination of characters for the genus *Neothyonidium*.

Remarks. We refer the new species to *Neothyonidium* Deichmann, 1938 on the basis of the body form, cover of tube feet, near 20 tentacles of two sizes, form of the composite calcareous ring, and body wall table ossicles with two pillars. But we do so with reservation because of the atypical combination of two morphological characters: five very small tentacles and 13 larger ones; *Thyone*-like table ossicles in the body wall. These two characters distinguish *Neothyonidium(?) insolitum* O'Loughlin from all other *Neothyonidium* species.

Subfamily **Thyoninae** Panning, 1949*Hemithyone semperi* (Bell, 1884)

Table 1; appendix 1; figure 21

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_56, WAM station no 20, barcode 10001531, from -15.376537 124.192773 35 m to -15.376196 124.192071 35 m, 19 Mar 2015, WAM Z89055 (1).

Remarks. We have retained *Hemithyone semperi* (Bell, 1884) in family *Thyonidae* and subfamily *Thyoninae*, but with major reservations. The species does have a composite calcareous ring, but the tube feet are radial and the species lacks table and cup ossicles and has predominantly very open fenestrated ellipsoids in the body wall. Smirnov (2012) remarked “it is possible that *Hemithyone* Pawson, 1963 does not belong to *Thyonidae*”. We await generic evidence for a review of its higher taxon referral.

Stolus canescens (Semper, 1867)

Table 1; appendix 1; figure 22

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_2, WAM station no 30, barcode 10002195, from -15.711306 124.315779 28 m to -15.71207 124.31566 28 m, 22 Mar 2015, WAM Z89056 (1).

Thyone Oken, 1815

Diagnosis (emended in O'Loughlin et al. 2012 from Pawson and Miller 1981). Tentacles 10; tube feet scattered on body wall, never restricted to radii; calcareous ring tubular with long posterior prolongations comprising a mosaic of small pieces; body wall ossicles tables with a spire of one or two pillars.

Type species. *Holothuria fusus* O. F. Müller, 1776 (monotypy).

Northern Australia species of *Thyone* reported in Rowe & Gates 1995 (type locality added). *T. axiologa* H. L. Clark, 1938 (Broome); *T. dura* Koehler & Vaney, 1908 (W India) (junior synonym *T. alba* H. L. Clark, 1938, by Heding 1940 (Broome)); *T. grisea* H. L. Clark, 1938 (Cape Bossut, N Australia); *T. micra* H. L. Clark, 1938 (Broome); *T. papuensis* Théel, 1886 (Torres Strait).

Remarks. We note in the Introduction the recent ruling by the ICZN that *Thyone* Oken, 1815 is now an available taxon. Pawson & Miller (1981) remarked on the need for a revision of the “supergen” *Thyone*. Arumugam (2012) has provided a morphological approach to the “management” of this “supergen”.

Liao & Clark (1995) noted that the holotype specimen of *Thyone papuensis* is now very damaged and completely decalcified. The original description and illustrations of the species are not sufficient for diagnostic comparisons and we thus provide (below) a description of specimens that we judge to be *Thyone papuensis*.

We add *Thyone pedata* Semper, 1867 to northern Australia species of *Thyone* on the basis of a specimen identified by us from Joseph Bonaparte Gulf (NMV F173267; UF tissue lot MOL AF 1537). We note that Rowe (in Rowe & Gates 1995)

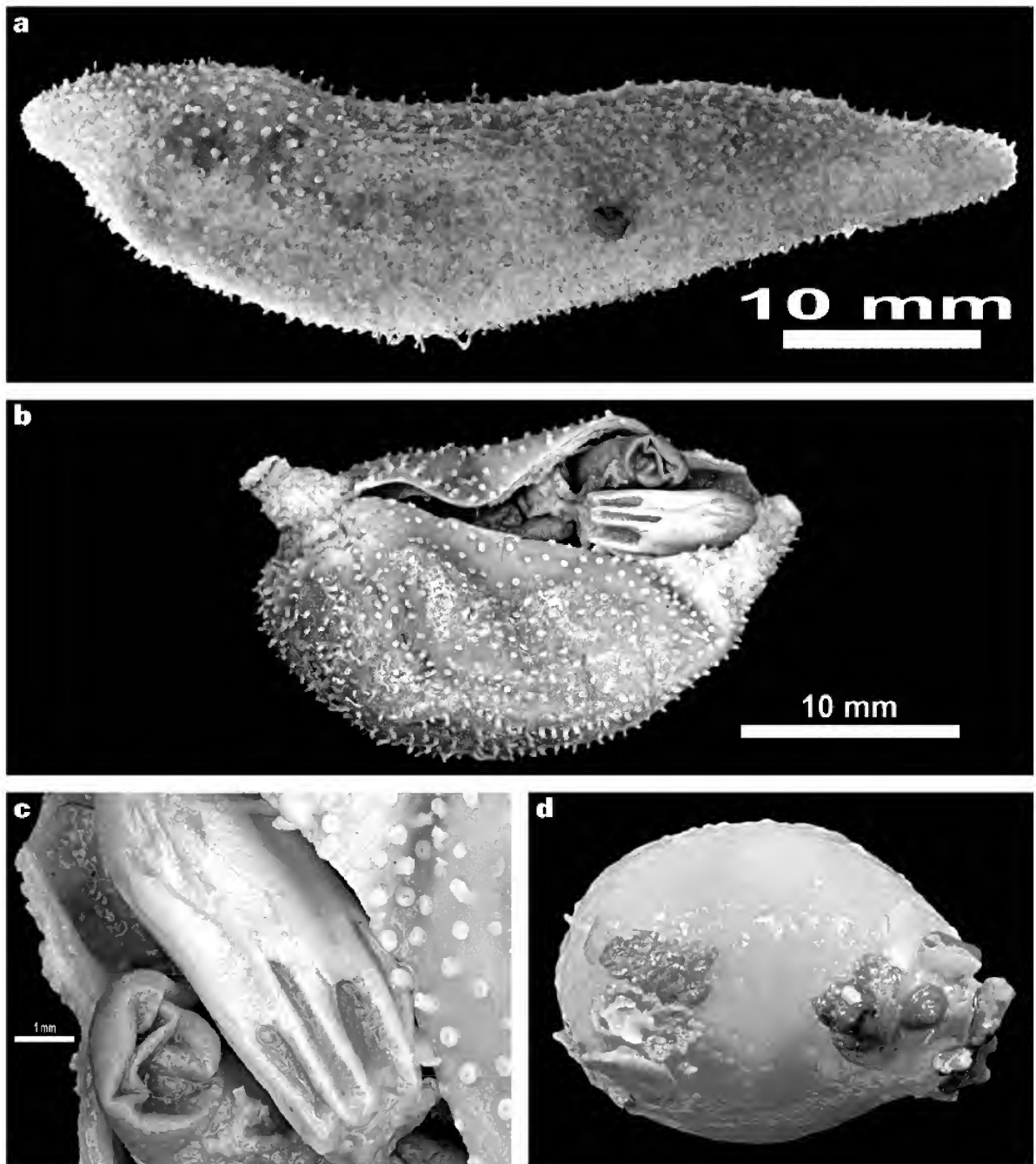


Figure 19. a–c, photos of holotype of *Neopsolidium(?) insolitum* O'Loughlin sp. nov. (WAM Z89054): a, photo of dorsal view of live holotype; b, photo of lateral view of preserved holotype; c, photo of calcareous ring of preserved holotype. d, photo of live specimen of *Massinium bonapartum* O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) (WAM Z89051; estimated 20 mm long live).

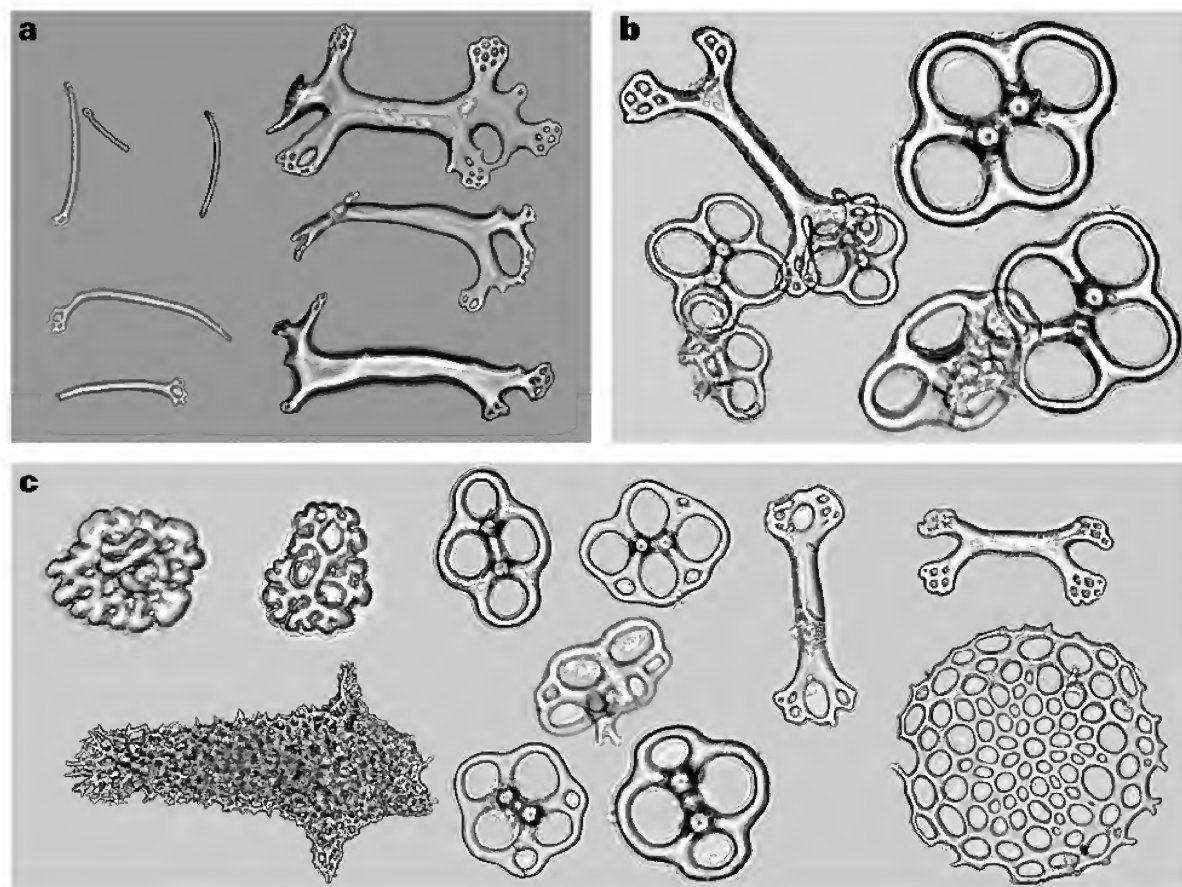


Figure 20. Ossicles from holotype of *Neopsolidium(?) insolitum* O'Loughlin sp. nov. (WAM Z89054): a, from tentacle, thick rods with widened and branched perforate ends up to 160 μm long, thin rods up to 90 μm long; b, from dorsal body wall, table discs up to 80 μm long, low two-pillar spires, distinctive tube foot support rod with bifurcate perforate ends; c, from posterior body wall, multi-layered scale fragment (bottom left), endplate up to 224 μm diameter (bottom right), distally widened and perforate tube foot support rods (top right), table discs up to 55 μm long (center), rosettes (top left).

referred *Thyone perissa* H. L. Clark, 1938 (WA) to *Massinium magnum* (Ludwig, 1882), and *Thyone minuta* H. L. Clark, 1938 to *Stolus minutus* (H. L. Clark, 1938).

Thyone papuensis Théel, 1886

Table 1; appendix 1; figures 23, 24

Thyone fusus var. *papuensis* Théel, 1886: 92, pl. 7 fig. 1.

Thyone papuensis H. L. Clark, 1921: 167.—1932: 221.—1946: 399.—Clark & Rowe, 1971: 182.—A. M. Clark, 1982: 489, 495, fig. 2.—Cannon & Silver, 1986: 32, fig. 9g.—Liao & Clark, 1995: 504, fig. 306.—Rowe (in Rowe & Gates), 1995: 316.

Type locality. Torres Strait.

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no LIN_6, WAM station no 16, barcode 10001097, from -15.27505 S 124.36988

E 46 m to -15.27543 S 124.36918 E 46 m, 18 Mar 2015, WAM Z89057 (1); RV *Solander*, sled, site no SOL_116a, WAM station no 18, barcode 10001259, from -15.26142 S 124.27518 E 41 m to -15.26172 S 124.27583 E 40 m, 18 Mar 2015, WAM Z89058 (1); RV *Solander*, sled, site no SOL_43, WAM station no 26, barcode 10002102, from -15.488461 124.201824 46 m to -15.488309 124.201113 46 m, 21 Mar 2015, WAM Z89059 (1) (ring eviscerated and lost); RV *Solander*, sled, site no SOL_77, WAM station no 34, barcode 10002542, from -15.725854 S 124.166978 41 m to -15.726405 124.16756 41 m, 23 Mar 2015, WAM Z89060 (1).

North Kimberley Region, near mouth of King George River, RV *Solander*, Sled 06, lot number (barcode) 023319, -13.8505 127.28868 45 m, 6 June 2013, WAM Z27863 (1) (UF tissue lot MOL AF 1463).

Description (Kimberley specimens; preserved in 95% ethanol). Body fusiform, narrow, with long tapers to narrow oral and anal ends, oral and anal ends may be slightly upturned, body (live) up to 35 mm long, up to 17 mm diameter; complete cover

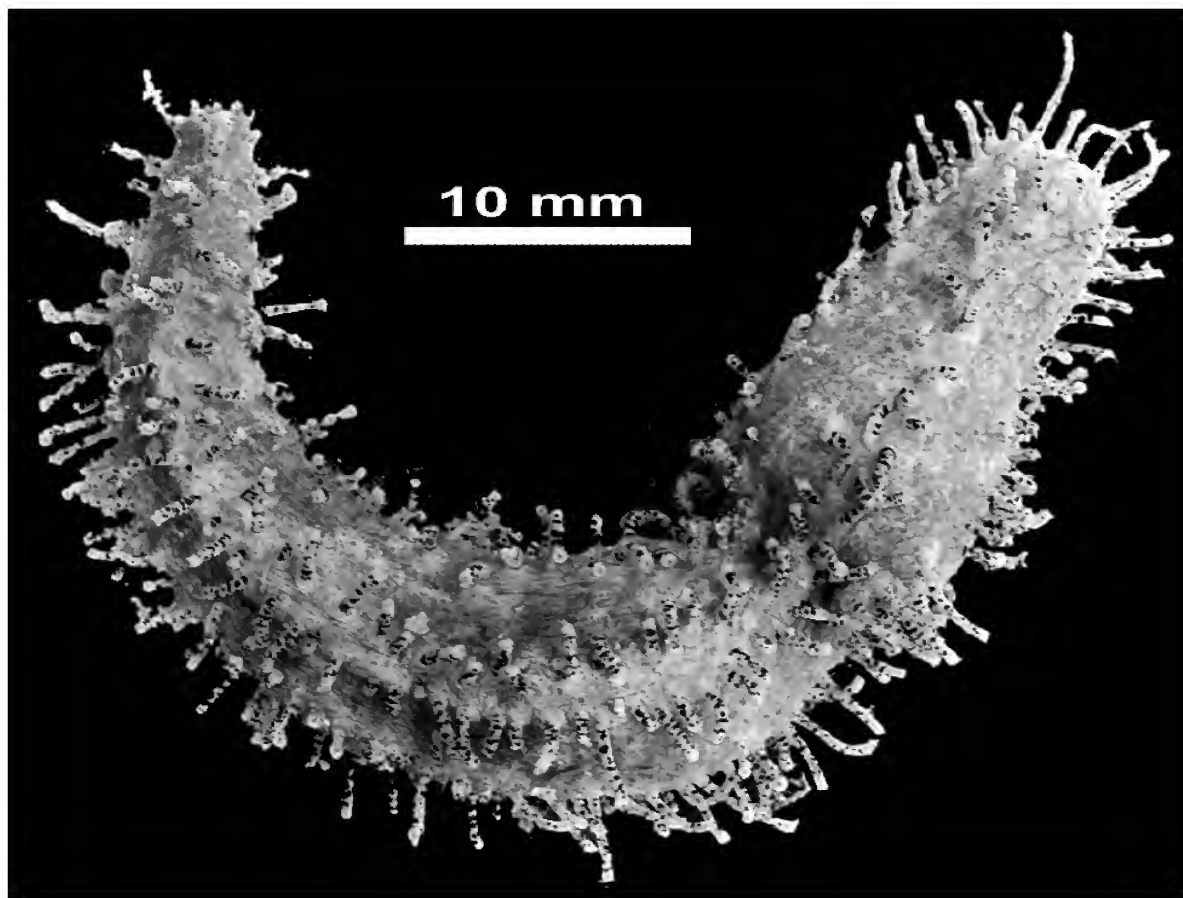


Figure 21. Photo of live specimen of *Hemithyone semperi* (Bell, 1884) (WAM Z89055).

of small tube feet, diameters about 0.2 mm, some in longitudinal series; 10 dendritic tentacles, two ventral small; calcareous ring tubular with long posterior prolongations comprising a mosaic of small pieces; inconspicuous anal scales present comprising thick single-layered plates with small perforation, multi-layered components, meshed rods component; single polian vesicle; gonad tubules not branched.

Mid-body ossicles scattered small tables with a spire of two pillars, discs with predominantly four perforations in smaller specimens, two larger central, two smaller distal, many discs in larger specimens with four or more smaller additional perforations, disc lengths commonly 50–55 μm , spire heights 23 μm , spires of two pillars, single apical bridge, apex of spire with two short pillar ends, each with a few blunt spines, spines sometimes with additional secondary spinelet. Tube feet endplates *Thyone*-like with small central perforations, outer ring of large perforations, marginal rim of small transversely oval perforation, endplates up to 110 μm diameter; support tables in tube feet with elongate, curved

discs up to about 120 μm long, four central perforations, single small perforation distally; spires with two pillars, joined apically with few blunt apical spines. Peri-anal body wall with single and multi-layered scale ossicles, tables with multi-perforate discs, tube foot support tables differing from mid-body. Tentacles and introvert with fine rods, tables and rosettes; largest rods with bifurcate ends, rods up to 90 μm long; table discs with many perforations, up to about 20; rosettes typically oval, about 30 μm long; rods and rosettes inter-grade in form.

Live colour pale brown to yellow with irregular red to brown patches on body and some tube feet; preserved colour off-white with red-brown to brown patches on body and some tube feet.

Distribution. North Western Australia, Kimberley Region, Camden Sound and King George River region, 40–46 m (this work); Houtman Abrolhos, WA, to Double Island Point, Queensland, 0–60 m (Rowe & Gates 1995).

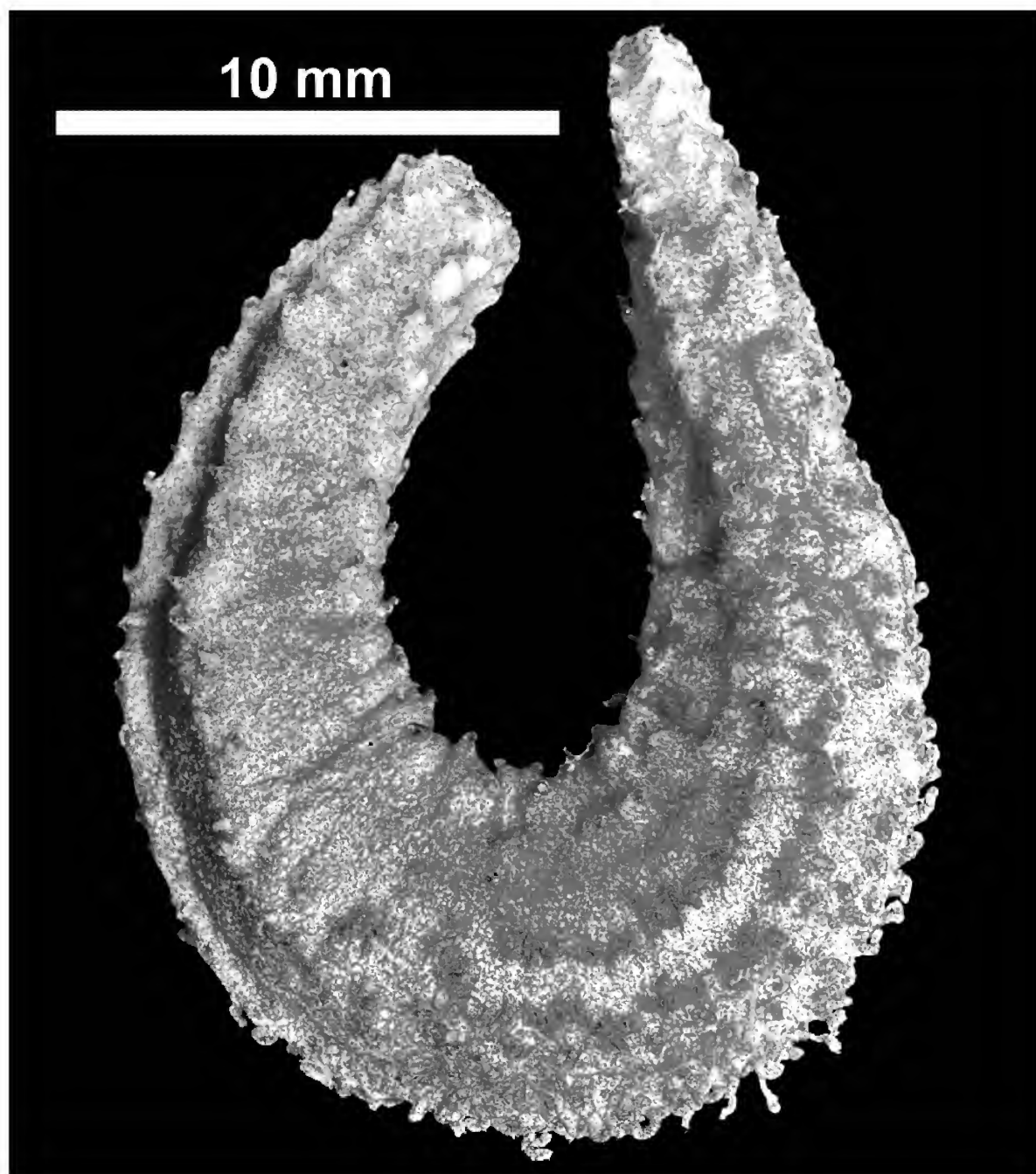


Figure 22. Photo of live specimen of *Stolus canescens* (Semper, 1867) (WAM Z89056).

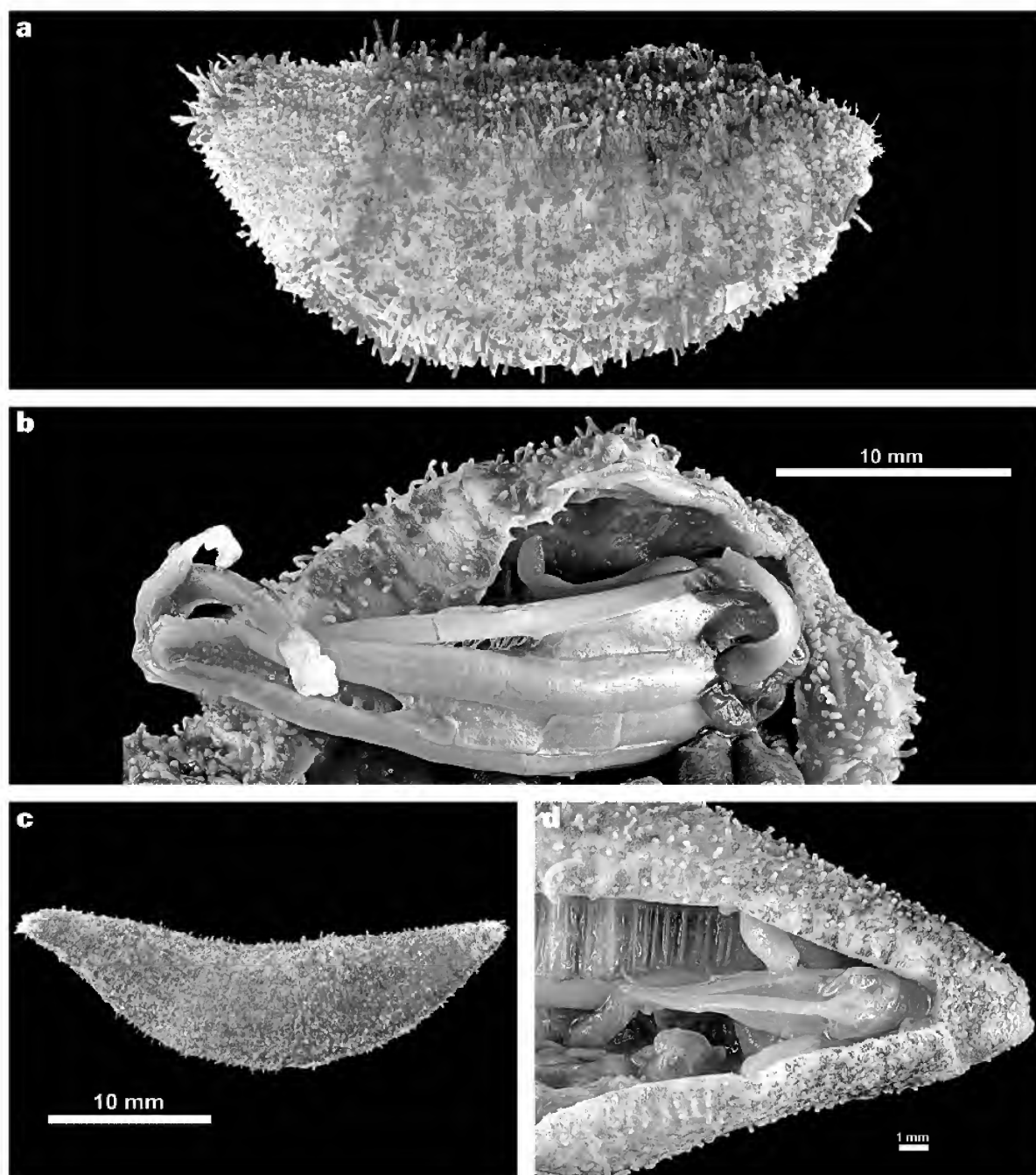


Figure 23. Photos of specimens judged to be *Thyone papuensis* Théel, 1886. a, lateral view of live specimen (WAM Z89060); b, calcareous ring of the same specimen preserved; c, lateral view of live specimen (WAM Z89058); d, calcareous ring of same specimen preserved (ring is relatively very small and is probably regenerating).

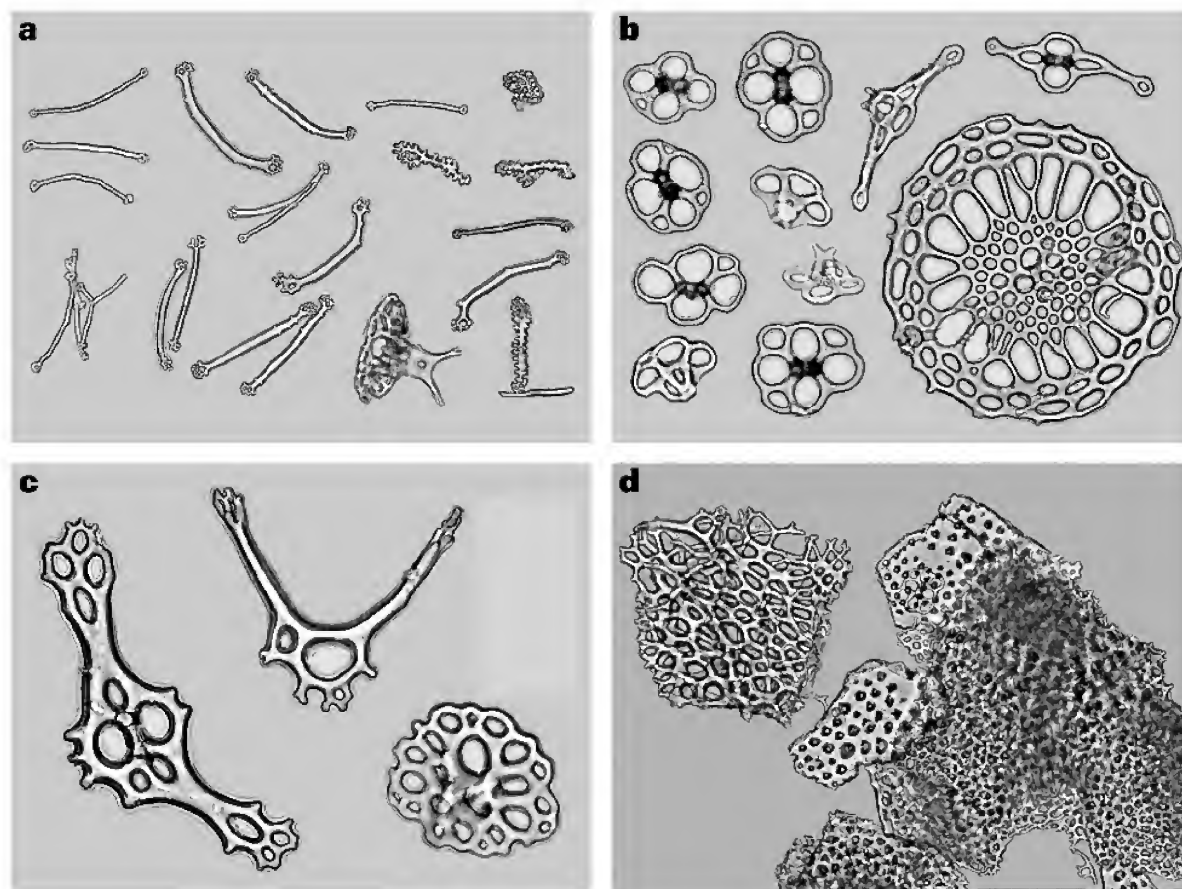


Figure 24. Photos of ossicles from *Thyone papuensis* Théel, 1886 specimens (WAM Z89057, WAM Z89058, WAM Z89059). a, from tentacle and introvert, fine rods (up to 90 μm long), rosettes (frequently about 30 μm long), table with multi-perforate disc and two spires; b, from mid-body wall and tube foot, table discs (frequently 50–55 μm long) and spires (about 23 μm high), endplate (up to 110 μm diameter), endplate support tables with single distal disc perforations (curved discs up to about 120 μm long); c, from peri-anal body wall, table with multi-perforate disc 56 μm across, tube foot support tables differing from body wall, upper one 80 μm between distal ends, lower left one 120 μm long; d, from peri-anal body wall, single and multi-layered fragments of scale ossicle.

Family **Thyonidiidae** Heding & Panning, 1954 (*sensu* Smirnov 2012)

Remarks. See O’Loughlin, Mackenzie & VandenSpiegel, 2014.

Actinocucumis Ludwig, 1875

Remarks. See O’Loughlin, Mackenzie & VandenSpiegel, 2014.

Actinocucumis longipedes H. L. Clark, 1938

Table 1; appendix 1; figure 25a

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_40, WAM station no 10, barcode 10000683, from -15.339415 124.160692 46 m to -15.33941 124.161459 46 m, 16 Mar 2015, WAM Z89061 (1).

Actinocucumis solanderi O’Loughlin, 2014 (in O’Loughlin, Mackenzie & VandenSpiegel, 2014)

Table 1; appendix 1; figure 25b

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no LIN_46, WAM station no 3, barcode 10000111, from -15.399083 124.345337 41 m to -15.398828 124.345572 42 m, 15 Mar 2015, WAM Z89062 (1); RV *Solander*, sled, site no LIN_36, WAM station no 17, barcode 10001112, from -15.220444 124.320894 50 m to -15.220159 124.320648 50 m, 18 Mar 2015, WAM Z89063 (1); RV *Solander*, sled, site no SOL_69, WAM station no 41, barcode 10002832, from -15.747648 124.146502 43 m to -15.747285 124.14634 43 m, 26 Mar 2015, WAM Z89064 (1).

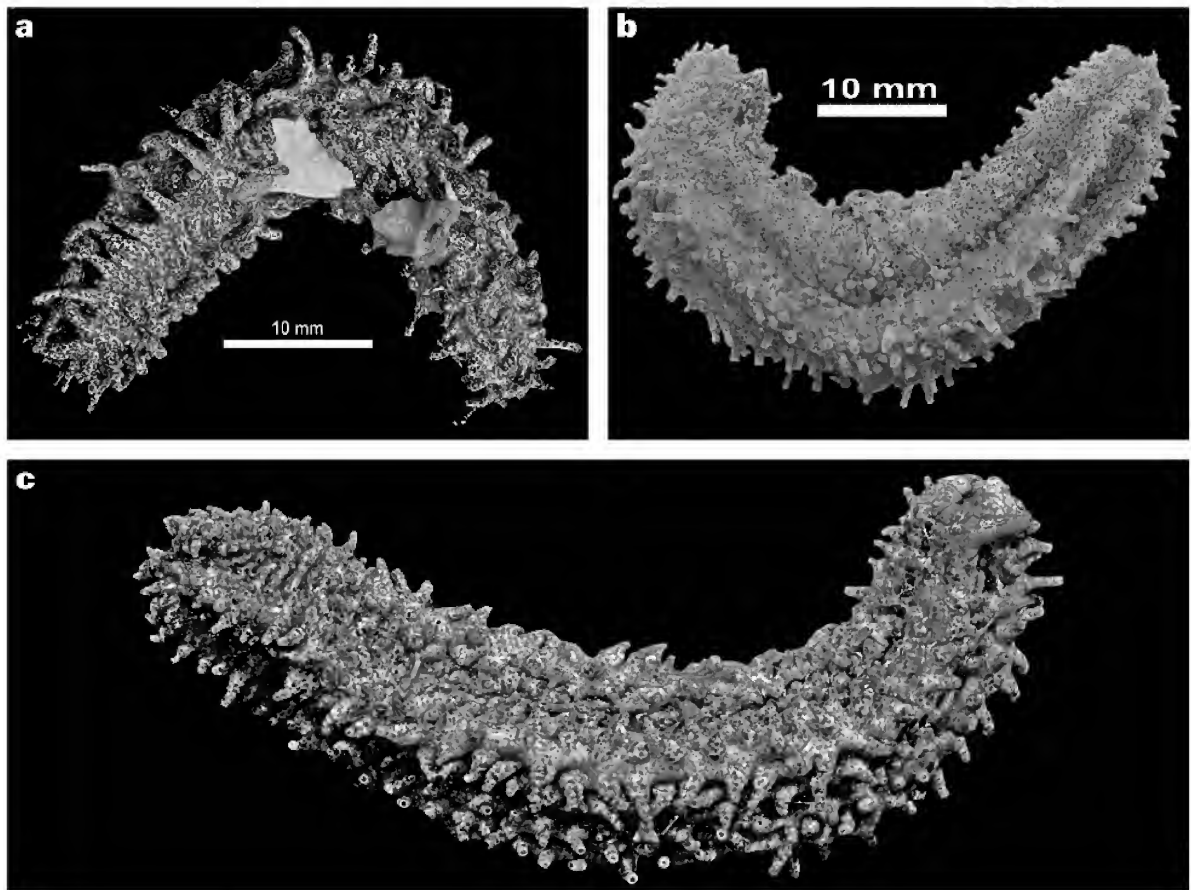


Figure 25. Photos of lateral views of live specimens of three species of *Actinocucumis* Ludwig, 1875: a, *Actinocucumis longipedes* H. L. Clark, 1938 (WAM Z89061); b, *Actinocucumis solanderi* O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) (WAM Z89063); c, *Actinocucumis typica* Ludwig, 1875 (WAM Z89065; estimated 25 mm long live).

***Actinocucumis typica* Ludwig, 1875**

Table 1; appendix 1; figure 25c

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_101, WAM station no 35, barcode 10002613, from -15.753636 124.270741 34 m to -15.75404 124.271287 34 m, 23 Mar 2015, WAM Z89065 (1); RV *Solander*, sled, site no SOL_97, WAM station no 39, barcode 10002792, from -15.782865 124.378047 32 m to -15.782335 124.378553 33 m, 25 Mar 2015, WAM Z89066 (1).

***Mensamaria intercedens* (Lampert, 1885)**

Table 1; appendix 1; figure 26

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_40, WAM station no 10, barcode 10000685, from -15.339415 124.160692 46 m to -15.33941 124.161459 46 m, 16 Mar 2015, WAM Z89067 (1); RV *Solander*, sled, site no SOL_32, WAM station no 19, barcode

10001307, from -15.253592 124.203038 45 m to -15.253318 124.202302 45 m, 19 Mar 2015, WAM Z89068 (1).

Order Molpadida Haeckel, 1896

Family Molpadiidae J. Müller, 1850

***Molpadia scabrum* (Sluiter, 1901)**

Table 1; appendix 1; figure 27a

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Linnaeus*, sled, site no LIN_48, barcode 53720, from -15.32474 124.42657 28 m to -15.32183 124.42742 12 m, 19 Mar 2015, WAM Z89069 (1).

Subclass Synaptacea Cuénot, 1891 (*sensu* Smirnov 2012)

Order Synaptida Cuénot, 1891 (*sensu* Smirnov 2012)

Family **Synaptidae** Burmeister, 1837 (*sensu* Östergren 1898)

Subfamily **Rynkatorpinae** Smirnov, 1989

Protankyra Östergren, 1898

Diagnosis (after Clark 1908). Tentacles digitate, 10–12, rarely 13 or 14; digits two on each side (rarely one only). Cartilaginous ring wanting. Polian vesicles 2–10, rarely one only. Stone canal usually single, rarely several. Stock of anchors more or less branched or only finely toothed; arms usually serrate; vertex of anchors without knobs. Anchor plates without a handle; with numerous irregular perforations, never with two large central perforations; with a more or less imperfectly developed bow across outer surface of posterior end; plates and perforations with either smooth or dentate margins.

Remarks. We have added “never with two large central perforations” to the diagnosis of anchor plates to distinguish *Protankyra* from genus *Rynkatorpa* Rowe & Pawson, 1967.

Protankyra insolens (Théel, 1886)

Table 1; appendix 1; figure 27b

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_107, WAM station no 1, barcode 10000038, from -15.514826 124.183111 46 m to -15.514503 124.183774 45 m, 14 Mar 2015, WAM Z89070 (1).

Protankyra torquea O’Loughlin sp. nov.

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:94FD3258-AAE8-48F3-939F-444D8ECC70FD>

Table 1; appendix 1; figure 28

Material examined. Holotype. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_48, WAM station no 4, barcode 10000142, from -15.39822 124.28823 23.2 m to -15.39864 124.28950 28.6 m, 15 Mar 2015, WAM Z89071.

Description (preserved in 95% ethanol). Anterior end only of synaptid species, 26 mm long, up to 16 mm diameter; body wall firm to hard, thick, opaque, not translucent; tentacles 12, trunks elongate, each with two pairs of closely placed distal digits, distal end of tentacles with short, thick papilla-like end; four polian vesicles detected; ciliated funnels not detected at base of dorsal mesentery or along coelomic inter-radii; longitudinal muscles broad, thick, rounded, undivided.

Body wall ossicles anchors, anchor plates, short rods, miliary granules. Anchors irregular in form, similar sizes, up to 304 μ m long, base of stocks variably indented, variably finely toothed, lateral ends of stock with raised rounded elevations, shaft variably constricted near base, anchor vertex lacking knobs, arms with 3–5 outer anteriorly pointed spines. Anchor plates irregularly heart-shaped, breadth and height sub-equal, size slightly variable, plates 230–260 μ m long, perforations (excluding basally) up to about 30, irregular in size, basal perforations numerous and small, fine teeth on inner margin of perforations numerous to rare to absent, plates

lacking significantly larger central perforations, margin of plates incomplete and irregular, irregular bow across posterior end of plates. Short curved rods abundant, of variable form, some curved inwards distally, some with distal swellings, some bluntly denticulate on inner margin, rods up to about 30 μ m long. Some miliary ‘granules’ found in body wall, not abundant, thin oval flat plates, some dumbbell shaped, up to about 30 μ m long. Tentacles with miliary ‘granules’ and rods, as in body wall. Longitudinal muscles with abundant miliary ‘granules’ only, ‘granules’ as in body wall and tentacles.

Live body colour off-white with irregular red-brown transverse patches, tentacle trunks as for body, digits pale yellow; preserved body colour off-white with irregular pale brown patches.

Distribution. Northwest Western Australia, Kimberley Region, Camden Sound, 23–29 m.

Etymology. Named *torquea* from the Latin *torqueo* (irregular), with reference to the irregular form of the typically incomplete margin of anchor plates, and irregular form of the anchor stock bases.

Remarks. The specimen comprises an anterior end only, is strongly contracted, and the alimentary canal and mesentery are mostly eviscerated. These factors might account for the apparent absence of ciliated funnels. Three *Protankyra* species are reported from northern Australia by Rowe (in Rowe & Gates 1995): *P. insolens* (Théel, 1886) (type locality Arafura Sea, north of Camden Sound); *P. similis* (Semper, 1867) (type locality the Philippines); *P. verrilli* (Théel, 1886) (type locality Torres Strait, NE Australia). Both *P. insolens* and *P. verrilli* were found in Camden Sound and are reported here. Each fits well with the description and illustration by Théel (1886). Amongst *Protankyra* species, *Protankyra torquea* O’Loughlin sp. nov. is closest to *P. verrilli* in morphological characters, but *P. verrilli* lacks rods in the body wall, is smaller, has a thin body wall, and lacks colour in the preserved state.

Protankyra verrilli (Théel, 1886)

Table 1; appendix 1; figure 27c

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_47, WAM station no 42, barcode 10002967, from -15.612805 124.073033 36 m to -15.612437 124.072883 35 m, 26 Mar 2015, WAM Z89072 (1).

Subfamily **Synaptinae** Burmeister, 1837 (*sensu* Smirnov 1989)

Synaptula lamperti Heding, 1928

Table 1; appendix 1; figure 29a

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no SOL_56, WAM station no 20, barcode 10001534, from -15.376537 124.192773 35 m to -15.376196 124.192071 35 m, 19 Mar 2015, WAM Z89073 (1).

Synaptula recta (Semper, 1867)

Table 1; appendix 1; figure 29b

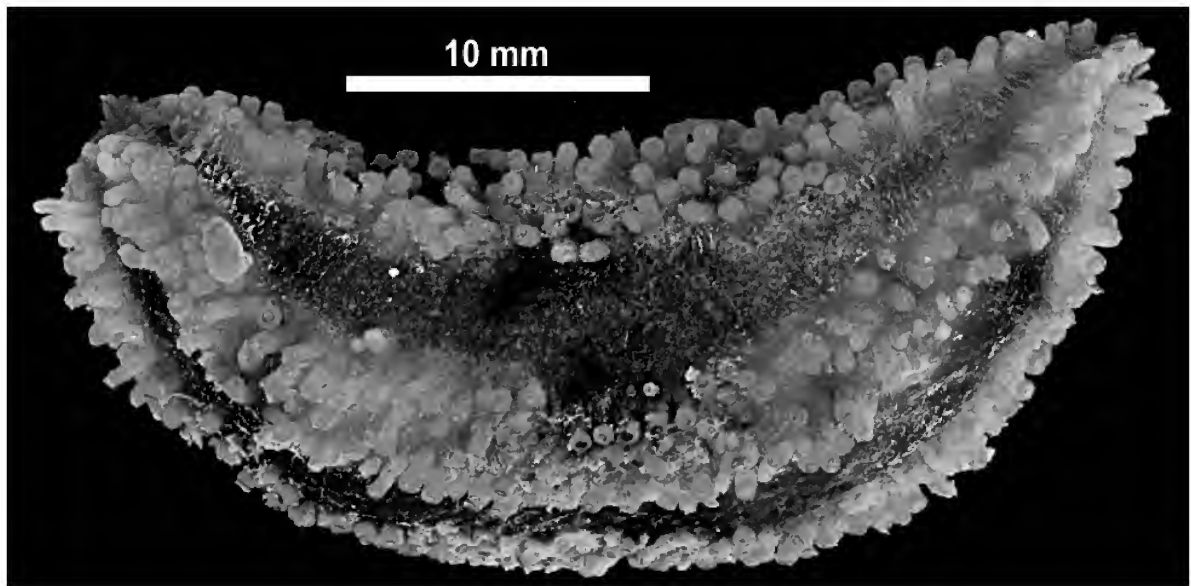


Figure 26. Photo of live specimen of *Mensamaria intercedens* (Lampert, 1885) (WAM Z89067).

Material examined. Northwest Western Australia, Kimberley Region, Camden Sound, WAMSI 1.1.1, RV *Solander*, sled, site no LIN_35, WAM station no 11, barcode 10000777, from -15.363088 124.443893 37 m to -15.362756 124.443995 37 m, 17 Mar 2015, WAM Z89074 (1); same data, barcode 10000919, WAM Z89075 (1).

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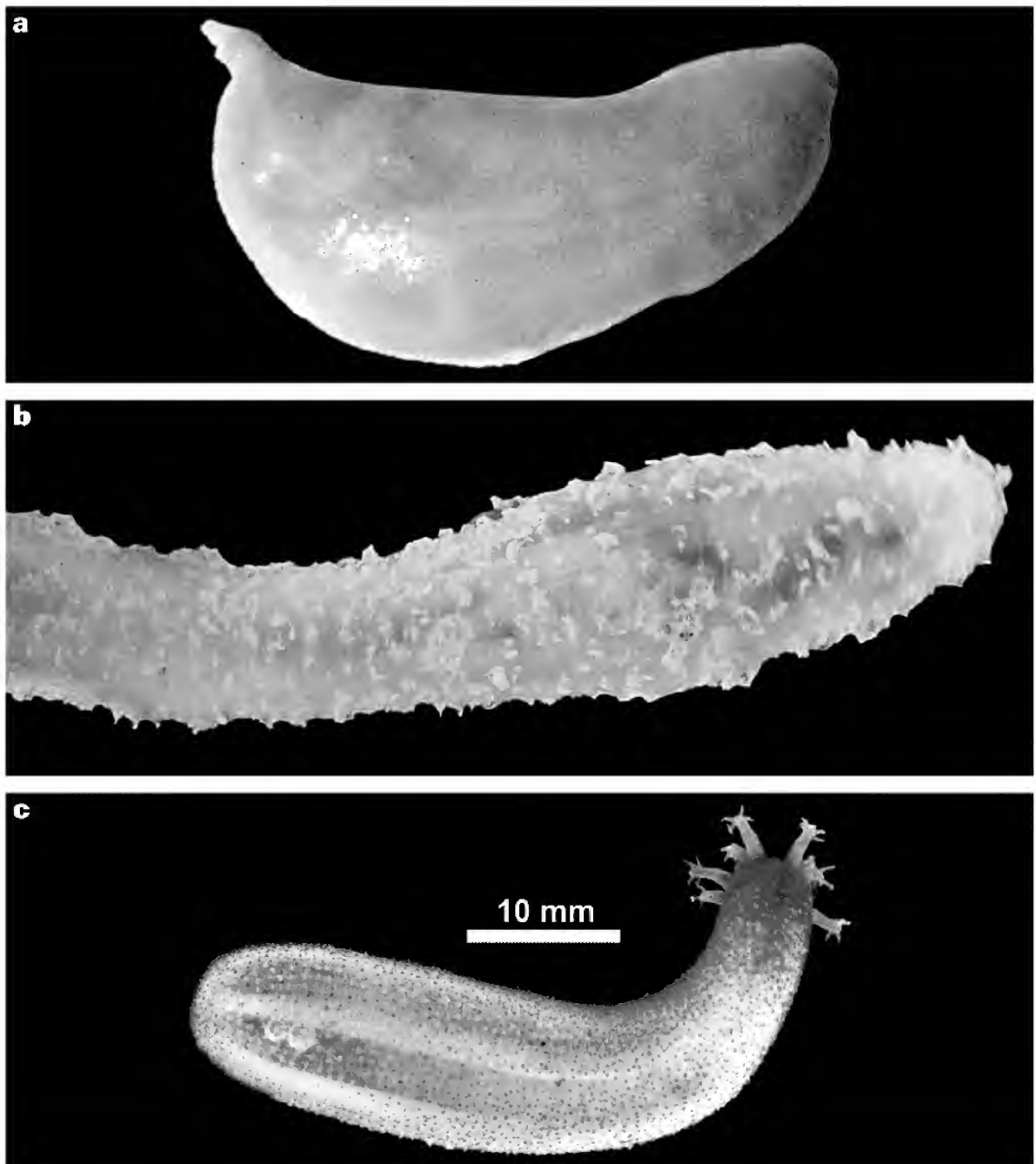


Figure 27. Photos of live specimens. a, *Molpadia scabrum* (Sluiter, 1901) (WAM Z89069; estimated 38 mm long live); b, *Protankyra insolens* (Théel, 1886) (WAM Z89070; estimated 24 mm long live); c, *Protankyra verrilli* (Théel, 1886) (WAM Z89072).

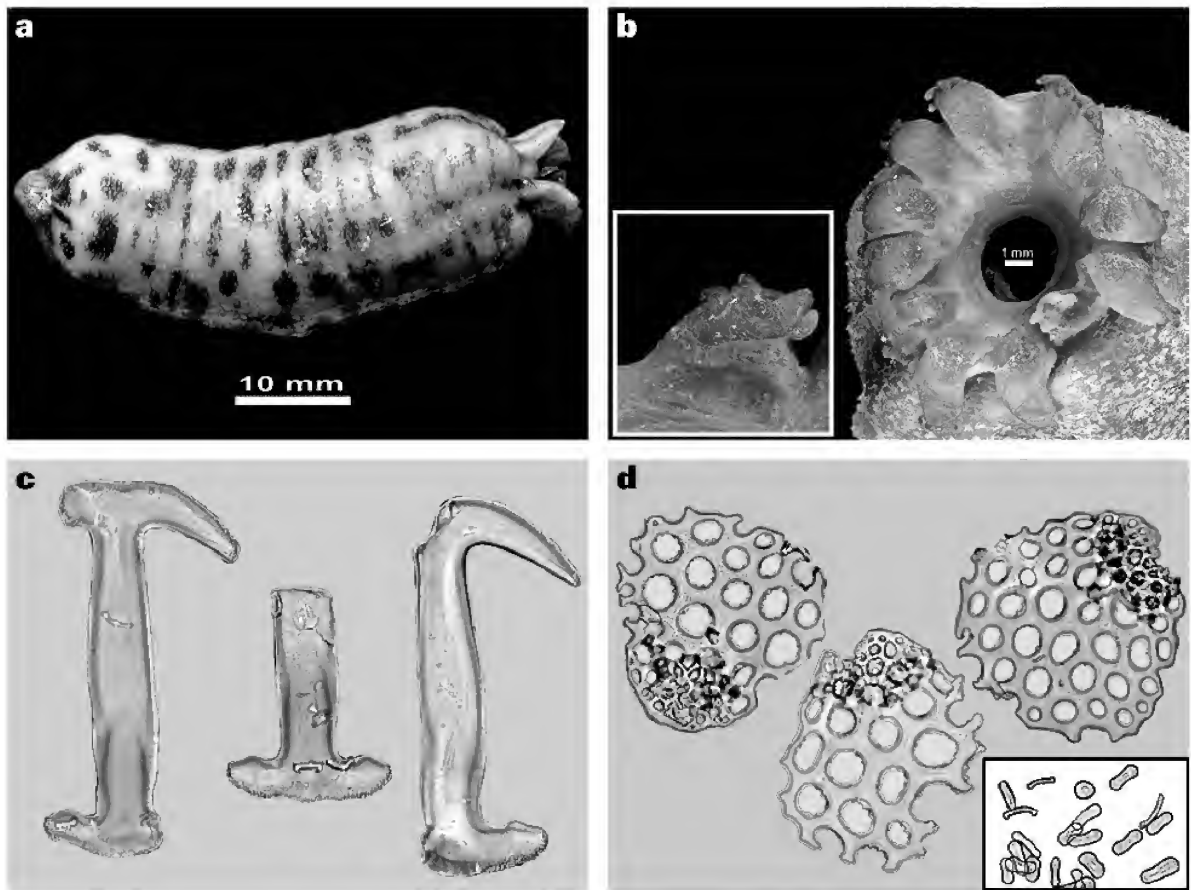


Figure 28. Photos of holotype of *Protankyra torquea* O'Loughlin sp. nov. (WAM Z89071): a, live holotype anterior fragment; b, photo of tentacle ring of preserved holotype (insert with a photo of one tentacle with two pairs of digits). c, d, ossicle photos from body wall of holotype: c, broken anchors, with some residual rods on surfaces (anchors up to 304 μm long); d, anchor plates (anchor plates 230–260 μm long); d insert, rods and miliary 'granules' about 30 μm long.

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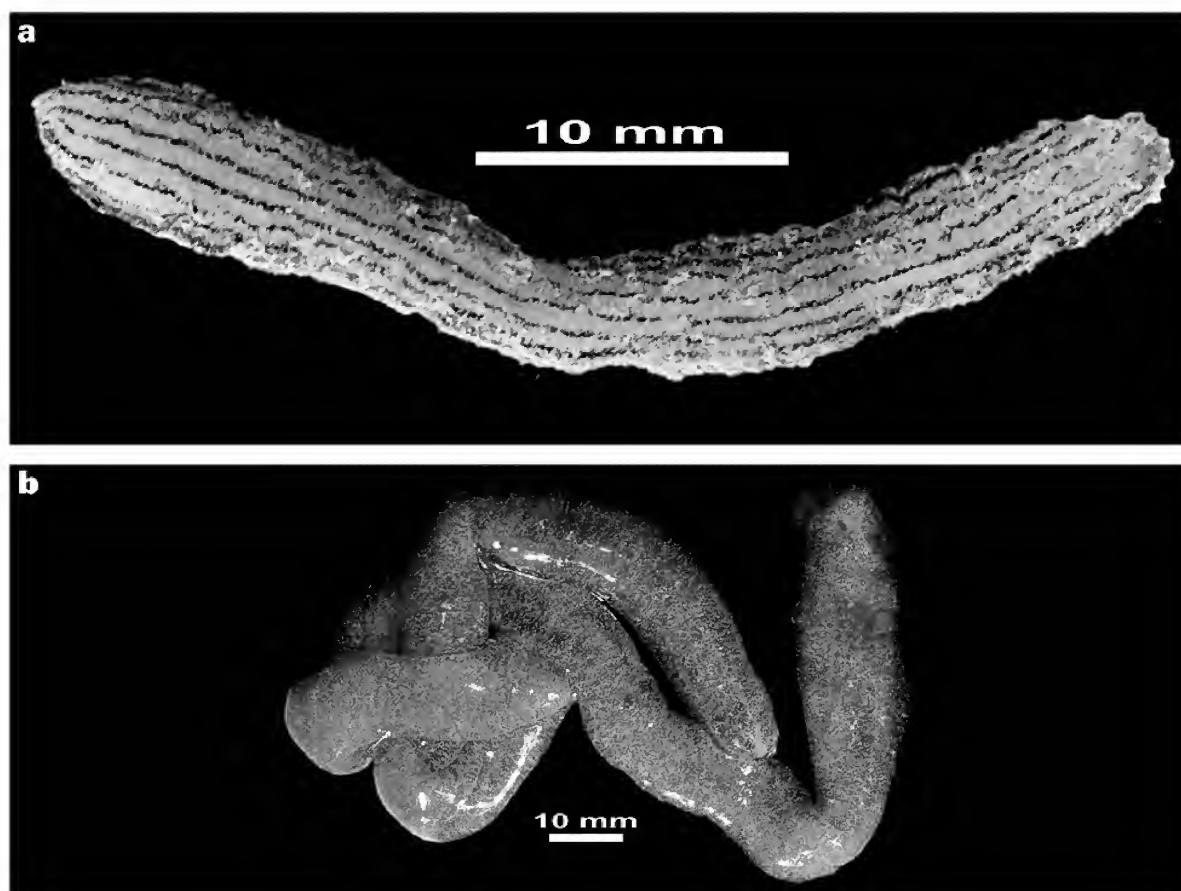


Figure 29. Photos of live specimens: a, *Synaptula lamperti* Heding, 1928 (WAM Z89073); b, *Synaptula recta* (Semper, 1867) (WAM Z89074).

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Appendix 1. Tissue samples for genetic data from Camden Sound sea cucumbers.

| Registration | Barcode | Type | Tissue | Taxa |
|--------------|----------|----------|--------|--|
| WAM | CSIRO | | MOLAF | |
| Z89000 | 10000043 | paratype | 1759 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89001 | 10000403 | paratype | 1760 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89002 | 10001168 | paratype | 1761 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89003 | 10001320 | paratype | 1762 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89004 | 10001821 | paratype | 1763 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89005 | 10001954 | paratype | 1764 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89006 | 10002938 | holotype | 1765 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89007 | 10002963 | paratype | 1766 | <i>Holothuria (Metriatyla) keesingi</i> O’Loughlin sp. nov. |
| Z89008 | No no. | | 1767 | <i>Holothuria (Thymiosyscia) gracilis</i> (Semper, 1868) |
| Z89009 | 10003037 | | 1768 | <i>Stichopus</i> unresolved species complex including <i>Stichopus hermanni</i> Semper, 1868 |
| Z89010 | 10003038 | | 1769 | <i>Stichopus</i> unresolved species complex including <i>Stichopus hermanni</i> Semper, 1868 |
| Z89011 | 10001261 | | 1770 | <i>Globosita elnaeae</i> O’Loughlin, 2014 (in O’Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89012 | 10001262 | | 1771 | <i>Globosita elnaeae</i> O’Loughlin, 2014 (in O’Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89013 | 10002087 | | 1772 | <i>Cercodemus anceps</i> Selenka, 1867 |
| Z89014 | 10000001 | | 1773 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89015 | 10000582 | | 1692 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89016 | 10000647 | | 1774 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89017 | 10001114 | | 1775 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89018 | 10001331 | | 1776 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89019 | 10001420 | | 1777 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89020 | 10001560 | | 1778 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89021 | 10001767 | | 1690 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89022 | 10001971 | | 1691 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89023 | 10002500 | | 1779 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89024 | 10002692 | | 1780 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89025 | 10002871 | | 1781 | <i>Colochirus quadrangularis</i> Troschel, 1846 |
| Z89026 | 10002268 | holotype | 1688 | <i>Plesiocolochirus minaeus</i> O’Loughlin sp. nov. |
| Z89027 | 53713 | | 1782 | <i>Leptopentacta grisea</i> H. L. Clark, 1938 |
| Z89028 | 10001662 | | 1783 | <i>Plesiocolochirus</i> sp. 1, unresolved species complex including <i>P. australis</i> (Ludwig, 1875) |
| Z89029 | 10001822 | | 1784 | <i>Plesiocolochirus</i> sp. 1, unresolved species complex including <i>P. australis</i> (Ludwig, 1875) |
| Z89030 | 10002101 | | 1785 | <i>Plesiocolochirus</i> sp. 1, unresolved species complex including <i>P. australis</i> (Ludwig, 1875) |
| Z89031 | 10000760 | | 1786 | <i>Pseudocolochirus axiologus</i> (H. L. Clark, 1914) |
| Z89032 | 10002389 | | 1787 | <i>Pseudocolochirus axiologus</i> (H. L. Clark, 1914) |
| Z89033 | 10001306 | | 1788 | <i>Phyllophorus (Phyllophorella) spiculata</i> Chang, 1935 |

| Registration | Barcode | Type | Tissue | Taxa |
|--------------|--------------|----------|---------------|--|
| WAM | CSIRO | | MOL AF | |
| Z89034 | 10000113 | | 1789 | <i>Phyllophorus (Urodemella) holothurioides</i> Ludwig, 1875 |
| Z89035 | 10001277 | | 1790 | <i>Phyllophorus (Urodemella) holothurioides</i> Ludwig, 1875 |
| Z89036 | 10000277 | | 1791 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89037 | 10000776 | | 1792 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89038 | 10001220 | | 1793 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89039 | 10001124 | | 1794 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89040 | 10001321 | | 1795 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89041 | 10001417 | | 1796 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89042 | 10001637 | | 1797 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89043 | 10001924 | | 1798 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89044 | 10002314 | | 1799 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89045 | 10002323 | | 1800 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89046 | 10002688 | | 1801 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89047 | 10002689 | | 1802 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89048 | 10002752 | | 1803 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89049 | 10002838 | | 1804 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89050 | 10002939 | | 1805 | <i>Havelockia versicolor</i> (Semper, 1867) |
| Z89051 | 10002243 | | 1806 | <i>Massinium bonapartum</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89052 | 10002725 | | 1807 | <i>Massinium bonapartum</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89053 | 10002966 | | 1808 | <i>Massinium bonapartum</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89054 | 10002958 | holotype | 1809 | <i>Neothyonidium(?) insolitum</i> O'Loughlin sp. nov. |
| Z89055 | 10001531 | | 1810 | <i>Hemithyone semperi</i> (Bell, 1884) |
| Z89056 | 10002195 | | 1811 | <i>Stolus canescens</i> (Semper, 1867) |
| Z89057 | 10001097 | | 1812 | <i>Thyone papuensis</i> Théel, 1886 |
| Z89058 | 10001259 | | 1813 | <i>Thyone papuensis</i> Théel, 1886 |
| Z89059 | 10002102 | | 1814 | <i>Thyone papuensis</i> Théel, 1886 |
| Z89060 | 10002542 | | 1815 | <i>Thyone papuensis</i> Théel, 1886 |
| Z89061 | 10000683 | | 1816 | <i>Actinocucumis longipedes</i> H. L. Clark, 1938 |
| Z89062 | 10000111 | | 1817 | <i>Actinocucumis solanderi</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89063 | 10001112 | | 1818 | <i>Actinocucumis solanderi</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89064 | 10002832 | | 1819 | <i>Actinocucumis solanderi</i> O'Loughlin, 2014 (in O'Loughlin, Mackenzie & VandenSpiegel, 2014) |
| Z89065 | 10002613 | | 1820 | <i>Actinocucumis typica</i> Ludwig, 1875 |
| Z89066 | 10002792 | | 1821 | <i>Actinocucumis typica</i> Ludwig, 1875 |
| Z89067 | 10000685 | | 1822 | <i>Mensamaria intercedens</i> (Lampert, 1885) |
| Z89068 | 10001307 | | 1823 | <i>Mensamaria intercedens</i> (Lampert, 1885) |
| Z89069 | 53720 | | 1824 | <i>Molpadia scabrum</i> (Sluiter, 1901) |
| Z89070 | 10000038 | | 1825 | <i>Protankyra insolens</i> (Théel, 1886) |
| Z89071 | 10000142 | holotype | 1826 | <i>Protankyra torquea</i> O'Loughlin sp. nov. |
| Z89072 | 10002967 | | 1827 | <i>Protankyra verrilli</i> (Théel, 1886) |
| Z89073 | 10001534 | | 1828 | <i>Synaptula lamperti</i> Heding, 1928 |
| Z89074 | 10000777 | | 1829 | <i>Synaptula recta</i> (Semper, 1867) |
| Z89075 | 10000919 | | 1830 | <i>Synaptula recta</i> (Semper, 1867) |
| Z89076 | 10002614 | | 1831 | indeterminate unknown species (ring and tentacles eviscerated) |

Appendix 2. List of tissues (with tissue sample code numbers, specimen repositories, specimen registration numbers, specimen source locations, and GenBank Accession numbers) from *Colochirus* Troschel, 1846 and *Plesiocolochirus* Cherbonnier, 1946 specimens with sequences in the phylogenetic tree.

| Genus | species | Tissue code | Museum | Registration | Location | GenBank |
|-------------------------|-------------------------|--------------|--------|--------------|---------------|----------|
| <i>Colochirus</i> | species 1 GP | UF 10059 | UF | 10059 | Heron Island | KX844560 |
| <i>Colochirus</i> | species 1 GP | MOLAF 1263 | QM | G22502 (1) | Lizard Island | KX844598 |
| <i>Colochirus</i> | species 1 GP | MOLAF 1264 | QM | G22502 (2) | Lizard Island | KX844574 |
| <i>Colochirus</i> | species 1 GP | MOLAF 1265 | QM | G22502 (3) | Lizard Island | KX844583 |
| <i>Colochirus</i> | species 1 GP | UF 8504 | UF | UF8504 | Lizard Island | KX844613 |
| <i>Colochirus</i> | species 1 GP | UF 2249 | UF | UF2249 | PNG | KX844564 |
| <i>Colochirus</i> | species 1 GP | UF 10918 | UF | UF10918 | Okinawa | KX844566 |
| <i>Colochirus</i> | species 1 GP | PH-28 | UF | 17852 | Philippines | KX844572 |
| <i>Colochirus</i> | species 1 GP | PH-34 | UF | 17853 | Philippines | KX844573 |
| <i>Colochirus</i> | species 1 GP | UF 957 | UF | 957 | Okinawa | KX844569 |
| <i>Colochirus</i> | species 1 GP | MOLAF 1200 | WAM | Z26234 (11) | Kimberley | KX844568 |
| <i>Colochirus</i> | species 1 GP | UF 7400 | UF | 7400 | Madagascar | KX844611 |
| <i>Colochirus</i> | species 1 GP | UF 7510 | UF | 7510 | Madagascar | KX844609 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1693 | NMV | F201782 | N Australia | KX844576 |
| <i>Colochirus</i> | <i>quadrangularis</i> | UF 13683 | UF | 13683 | Singapore | KX844595 |
| <i>Colochirus</i> | <i>quadrangularis</i> | UF 13667 | UF | 13667 | Singapore | KX844565 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1692 | WAM | Z89015 | Kimberley | KX844610 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 398 | NMV | F149742 | Kimberley | KX844559 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1691 | WAM | Z89022 | Kimberley | KX844596 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1690 | WAM | Z89021 | Kimberley | KX844594 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1453 | WAM | Z27858 | Kimberley | KX844605 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1209 | NMV | F173259 | N Australia | KX844601 |
| <i>Colochirus</i> | <i>quadrangularis</i> | MOLAF 1210 | NMV | F173260 | N Australia | KX844562 |
| <i>Colochirus</i> | <i>quadrangularis</i> | QM09 058 | QM | SBD503854 | Queensland | KX844586 |
| <i>Colochirus</i> | <i>quadrangularis</i> | QM09 074 | QM | TS80000215 | Queensland | KX844577 |
| <i>Colochirus</i> | <i>robustus</i> | MOLAF 396 | NMV | F149737 | Kimberley | KX844579 |
| <i>Colochirus</i> | <i>robustus</i> | MOLAF 397 | NMV | F149738 | Kimberley | KX844606 |
| <i>Colochirus</i> | <i>robustus</i> | UF 17373 | UF | 17373 | Philippines | KX844561 |
| <i>Colochirus</i> | <i>robustus</i> | UF 17672 | UF | 17672 | Philippines | KX844582 |
| <i>Plesiocolochirus</i> | <i>challengeri</i> | MOLAF 1460 | NMV | F203000 | Kimberley | KX844597 |
| <i>Plesiocolochirus</i> | <i>challengeri</i> | MOLAF 1461 | WAM | Z27862 | Kimberley | KX844570 |
| <i>Plesiocolochirus</i> | <i>challengeri</i> | MOLAF 1213 | NMV | F173263 | N Australia | KX844587 |
| <i>Plesiocolochirus</i> | species 2 GP | UF 10077 | UF | 10077 | Heron Island | KX844571 |
| <i>Plesiocolochirus</i> | species 2 GP | UF 9986 | UF | 9986 | Heron Island | KX844563 |
| <i>Plesiocolochirus</i> | species 2 GP | UF 10041 | UF | 10041 | Heron Island | KX844607 |
| <i>Plesiocolochirus</i> | <i>tessellaris</i> | MRAC 2005 39 | MRAC | 2616 | Comoros | KX844590 |
| <i>Plesiocolochirus</i> | species 1 GP | MOLAF 394 | NMV | F150795 | Kimberley | KX844567 |
| <i>Plesiocolochirus</i> | species 1 GP | MOLAF 395 | NMV | F150805 | Kimberley | KX844604 |
| <i>Plesiocolochirus</i> | species 1 GP | MOLAF 1444 | WAM | Z27854 (1) | Kimberley | KX844584 |
| <i>Plesiocolochirus</i> | species 1 GP | MOLAF 1443 | WAM | Z27854 (2) | Kimberley | KX844578 |
| <i>Plesiocolochirus</i> | species 1 GP | MOLAF 1196 | WAM | Z26229 (3) | Kimberley | KX844585 |
| <i>Plesiocolochirus</i> | species 1 GP | UF 8952A | UF | 8952A | Palau | KX844589 |
| <i>Plesiocolochirus</i> | species 1 GP | UF 9535 | UF | 9535 | Ningaloo | KX844612 |
| <i>Plesiocolochirus</i> | species 1 GP | UF 17730 | UF | 17730 | Japan | KX844575 |
| <i>Plesiocolochirus</i> | <i>minaeus</i> sp. nov. | MOLAF 1688 | WAM | Z89026 | Kimberley | KX844602 |

| Genus | species | Tissue code | Museum | Registration | Location | GenBank |
|-------------------------|----------------|--------------------|---------------|---------------------|-----------------|----------------|
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 430 | NMV | F151840 (1) | Victoria | KX844592 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 431 | NMV | F151840 (2) | Victoria | KX844603 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 1175 | NMV | F173252 | Victoria | KX844593 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 1177 | NMV | F173255 (2) | Victoria | KX844588 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 453 | NMV | F125377 | Victoria | KX844591 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 454 | NMV | F125376 | Victoria | KX844580 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 450 | NMV | F126892 (1) | Victoria | KX844600 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 451 | NMV | F126892 (2) | Victoria | KX844581 |
| <i>Plesiocolochirus</i> | <i>ignavus</i> | MOLAF 452 | NMV | F126892 (3) | Victoria | KX844599 |

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The *Discovery* Expedition sea cucumbers (Echinodermata: Holothuroidea)

(<http://zoobank.org/urn:lsid:zoobank.org:pub:7039F593-8FE2-4668-BBC9-E18F2D82F8F8>)

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Abstract

O'Loughlin P. M., Tavancheh, E. & Harding, C. 2016. The *Discovery* Expedition sea cucumbers (Echinodermata: Holothuroidea). *Memoirs of Museum Victoria* 75: 53–70.

Identifications of all lots of Holothuroidea specimens collected from February 1926 to January 1939 by the *Discovery* Expedition are listed with station data, locality and depth. This report includes identifications reported previously by Heding (in Heding & Panning), O'Loughlin & Ahearn, O'Loughlin *et al.* and O'Loughlin & VandenSpiegel. New taxa from the *Discovery* Expedition have been reported previously, and a summary is provided. The new taxa herein are for equatorial West Africa specimens: new genus *Cucusquama* O'Loughlin and new species *Cucusquama wesafrica* O'Loughlin. Systematic notes are provided for genera *Clarkiella* Heding (in Heding & Panning) and *Echinopsolus* Gutt, and species *Ocnus capensis* (Théel), genera *Parathyonidium* Heding (in Heding & Panning) and *Pentactella* Verrill, and species *Psolus dubiosus* Ludwig & Heding, *Psolus lockhartae* O'Loughlin & Whitfield and *Sigmodota contorta* (Ludwig). Earlier echinoderm specialists who studied *Discovery* Expedition holothuroids are acknowledged: Cynthia Ahearn, Elizabeth Deichmann, Svend Heding, Melanie Mackenzie, Albert Panning and Emily Whitfield.

Keywords

Falkland Islands, New Zealand, Ross Sea, South Georgia, West Africa, *Clarkiella*, *Echinopsolus*, *Parathyonidium*, *Pentactella*, *Psolus*, new genus, new species.

Introduction

In 1918 an *Interdepartmental Committee on Research and Development in the Falkland Islands Dependencies* was formed. Its report to the British Parliament in 1920 resulted in the appointment of a *Discovery Committee* in 1923. The first *Discovery* Expedition sailed south on 24 September 1925 aboard Robert Falcon Scott's *Discovery* as its research vessel (Figure 1a). It had been built for Scott's 1901–1904 *British National Antarctic Expedition*. In the Falklands it was found to be unsuitable for scientific operations in open waters. The *William Scoresby* (Figure 2) was built in 1925 and was used principally in whale research. A marine biological station (known as *Discovery House*) was built at King Edward Point on South Georgia. In 1927 the *Discovery II* (Figure 1b) was built and was judged to be an outstanding success. The *Discovery Committee* was dissolved in 1949 when it became part of the National Institute of Oceanography, located in Surrey, UK. The Whale Research Unit moved, briefly, to the Natural History Museum in London. It later became part of the British Antarctic Survey (BAS), based in Cambridge. In 1995 the Institute of Oceanographic Sciences became part of the Southampton Oceanography Centre. Scott's second

Antarctic expedition on the *Terra Nova* (1910–1913) collected marine invertebrate animals amongst which was a large collection of sea cucumbers. This *Terra Nova* sea cucumber collection is referred to below.

The results of the *Discovery* Expedition have been documented in the 37 volumes of *Discovery Reports* (1928–1980). The ships used in the early decades of the Expedition were the RRS *Discovery I* (Figure 1a; from 25 September 1925 to 1927), RRS *Discovery II* (Figure 1b; five voyages from 1929 to 1935, and sixth voyage in 1950), and RRS *William Scoresby* (Figure 2, eight voyages from 1926 to 1951). The localities visited by the Expedition were predominantly the Falkland Islands and Falkland Islands Dependencies (South Georgia, S. Sandwich Is, S. Shetland Is, S. Orkney Is) and the Ross Sea. Some collections were made from the Marine Biological Station (*Discovery House*) at King Edward Point, South Georgia. Some collections were made during voyages to and from the Falkland Islands. Thus species identifications are included here for Antipodes I., Balleny I., the Haakon VII Sea, Marion I., New Zealand, the Ross Sea, Marine Station 82 in Saldanha Bay in south-west Africa, and equatorial west Africa.



Figure 1. Ships from which the early *Discovery* Expedition was conducted. a, Scott's RRS *Discovery I* (collected from 25 Sep 1925 to 1927); b, RRS *Discovery II* (collected for five voyages from 1929 to 1935, and a sixth voyage in 1950).

The *Discovery* Expedition to the South Sandwich Islands in 1927 was not conducted by RRS *Discovery* or RRS *William Scoresby*, and is reported in *Discovery* Report Vol. 3. The *Discovery* Expedition to the Ross Sea from Nov. 1928 to Feb. 1929 was not conducted by RRS *Discovery* or RRS *William Scoresby*, and is reported in *Discovery* Report Vol. 3. There are no holothuroid lots from these expeditions in the collection reported here. The *British Antarctic Survey* commenced its survey of the Falkland Islands Dependencies in 1943, and the BAS surveys continue to the present day.

Three papers have been published in the *Discovery* Reports on the early echinoderm collections. Mortensen (1936, Vol. 12) reported on the *Discovery* Echinoidea and Ophiuroidea collected from 1925 to 1935. Dilwyn John (1938, in Vol. 18) reported on the *Discovery* Crinoidea collected from 1935 to 1937. Fisher (1940, in Vol. 20 issued in 1941) reported on the *Discovery* Asteroidea collected from 1925 to 1936. Some *Discovery* Expedition Holothuroidea have been reported in Heding & Panning (1954), O'Loughlin & Ahearn (2008),

O'Loughlin & VandenSpiegel (2010) and O'Loughlin *et al.* (2014). This paper includes these taxa reported previously, and is the first comprehensive *Discovery* report on the Holothuroidea that were collected from 28 February 1926 to 30 January 1939.

The Danish holothuroid specialist Svend Geisler Heding (1902–1949, see Acknowledgments, Figure 3a) studied the *Discovery* Expedition holothurians in the Zoological Museum in the University of Copenhagen (ZMUC) until his death. He described two new genera and species: *Clarkiella discoveryi* Heding (in Heding & Panning 1954); *Parathyonidium incertum* Heding (in Heding & Panning 1954). These new taxa were ascribed to Heding posthumously by the German sea cucumber specialist Albert Panning (1894–1978, Figure 3b). Panning included the descriptions in Heding & Panning 1954 from Heding's notes and mentioned that he did this in collaboration with Elizabeth Deichmann (working at that time on the *Discovery* Expedition holothuroids in the Museum of Comparative Zoology at Harvard). The Heding types are lodged in London (NHMUK), Paris (MNHN) and Copenhagen (ZMUC) (see Table 2 below).

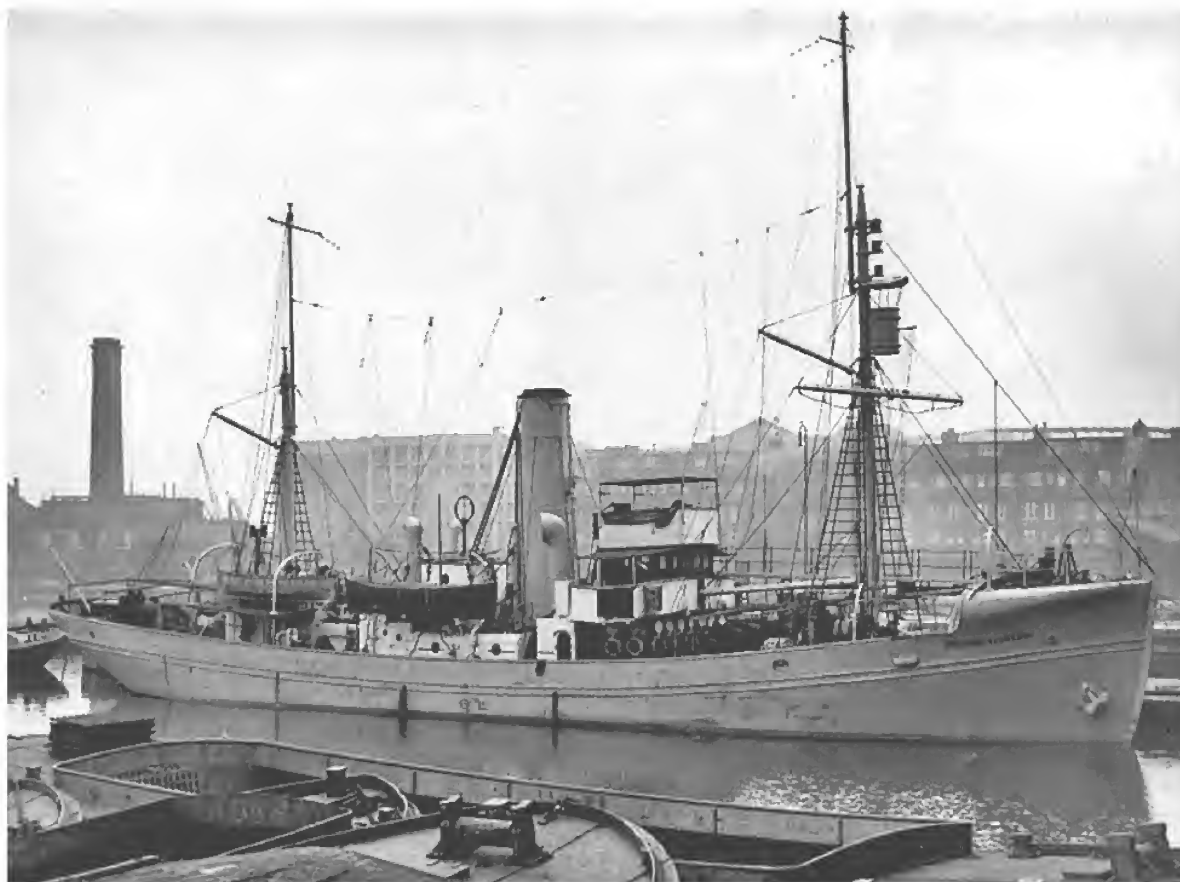


Figure 2. RRS *William Scoresby* served the *Discovery* Expedition for eight voyages from 1926 to 1951.

Shortly after Heding's death in 1949, H. W. Parker (the Keeper of Zoology in the British Museum) wrote on 25th July in 1950 to Elizabeth Deichmann (c/o F. Jensenius Madsen in the Zoology Museum in the University of Copenhagen) inviting her to work on the holothurians in the *Terra Nova*, *BANZARE* and *John Murray* collections. The letter noted that these collections belonged to the British Museum. She was also invited to consider contributing to the "Reports of the John Murray Expedition". The letter of invitation anticipated that Dr. Macintosh (in the National Institute of Oceanography that managed the *Discovery* collections) would probably also like Deichmann to study the *Discovery* Expedition holothurians and contribute to the *Discovery* Reports. These four collections were still in Copenhagen at the time. The letter notes that Dr. Madsen had the notes left by Heding. These notes were evidently passed on to Deichmann and were presumably the source from which Albert Panning published the new taxa that he ascribed to Heding. Shortly after this communication the collections were returned to the British Museum in London.

Elizabeth Deichmann (1896–1975, Figure 4a), like Heding, was Danish and a protégée of echinoderm specialist Theodor Mortensen (1868–1952). In 1929 Deichmann began working in The Museum of Comparative Zoology in Harvard University in Massachusetts. In response to the invitation to work on the four major holothuroid collections she visited London in 1950 to study the collections. A National Institute of Oceanography internal letter (David Pawson *pers. comm.*) of 7 August 1963, directed to Dr Macintosh, noted: "In Miss Ailsa Clark's absence in America (Miss Clark is in charge of Echinoderms), Dr Deichmann arranged with an assistant in the department to have a considerable part of the material packed up and sent over to Harvard. Unfortunately no list was made of the station numbers and species selected by Dr Deichmann, but I have asked Miss Clark to check what remains of the *Discovery* specimens in her department against my list of material originally sent to Heding. I enclose the full data on a separate sheet". This letter noted that the last communication with Deichmann was in 1961, and at the time of this communication (1963) she had retired from work at the MCZ, Harvard

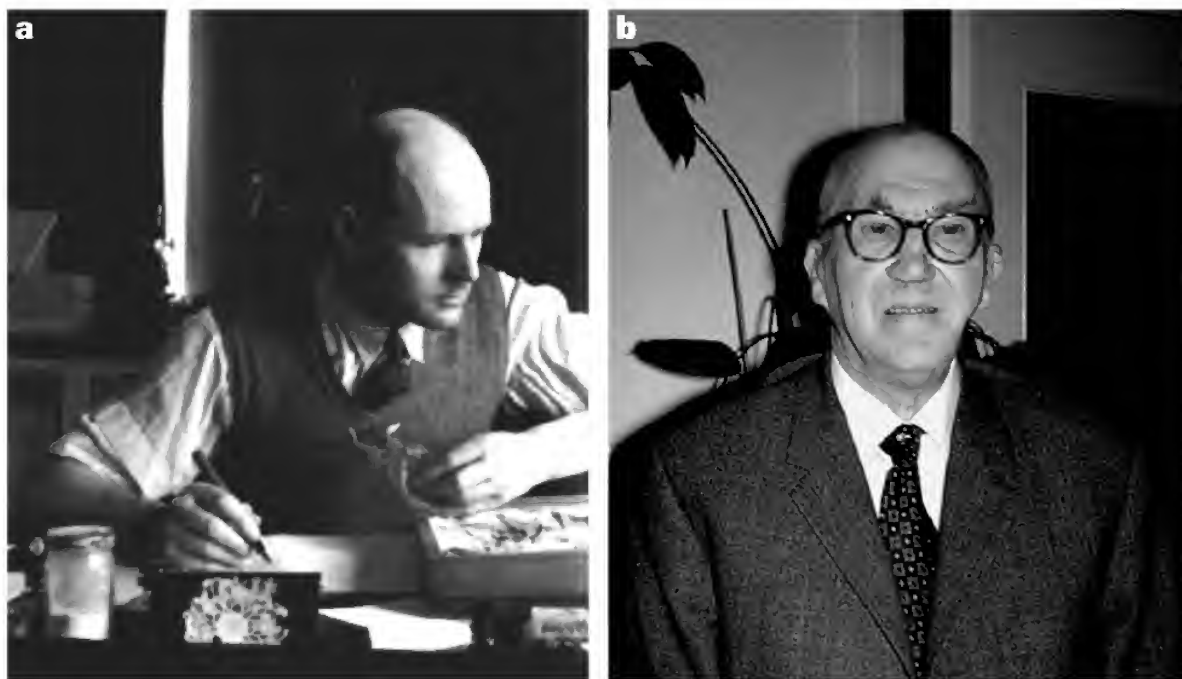


Figure 3. Authors who published the first new sea cucumber genera and species from the *Discovery* Expedition in their monograph on the Phyllophoridae in 1954. a, Danish holothuroid specialist Svend Geisler Heding (1902–1949; photo provided by Tom Schioette in ZMUC); b, German holothuroid specialist Albert Panning (1894–1978; photo provided by David Pawson in USNM).

University. But in a letter to David Pawson (*pers. comm.*) on 25 February 1967 it appears that she was still working at the MCZ and hoped to work with Pawson on the *Discovery* holothuroids. This did not eventuate. Deichmann published her last paper in 1958. None of her papers mentions any *Discovery* Expedition holothuroids.

The collections arrived at the MCZ in 1950. In a letter dated 25th February 1967 to David Pawson (Smithsonian Institution, *pers. comm.*), Deichmann commented that the collection was in poor condition when she received it and that localities were “somewhat mixed up”. But she wrote that she “got good help from Ailsa Clark” to resolve issues. Elizabeth further commented that she had made good headway and had a lot of notes about the genus *Psolus*. There was some evidence of Deichmann’s work when we received the collection in Museum Victoria (2008). Deichmann did not publish on any of the taxa or contribute to any report. Unfortunately we do not have her notes on *Psolus*.

Following Deichmann’s retirement the *Discovery* and *Terra Nova* collections were transported by David Pawson (*pers. comm.* probably in 1973) from the MCZ to the United States National Museum in Washington (Smithsonian Institution). In the Smithsonian an echinoderm specialist Cynthia (Gust) Ahearn (1952–2008, Figure 4b) identified many lots personally, and then collaboratively with Mark O’Loughlin. O’Loughlin & Ahearn (2008) included numerous lots of *Discovery* Expedition psolid species (see Table 3 below).

Ahearn had the *Discovery* holothuroid collection sent to Museum Victoria in 2008, with permission from the Natural History Museum (UK). Mark O’Loughlin, Melanie Mackenzie (Figure 4c) and Emily Whitfield (Figure 4d) then continued with identifications. This work was delayed in 2010 until related systematic issues were resolved. But O’Loughlin & VandenSpiegel (2010) included numerous *Discovery* synaptids (as apodids) in their comprehensive review (see Table 4 below). Identification by O’Loughlin in Museum Victoria recommenced in 2015, and identifications of the *Discovery* holothuroid lots have now been completed and earlier identifications changed or confirmed. The results are collated and reported here (see Table 1 below). Apart from the Heding types lodged in Copenhagen (ZMUC) and Paris (MNHN), the *Discovery* holothuroids are lodged in the NHMUK.

The *Discovery* Expedition holothuroid lots that are the subject of this report were collected in the 1920’s and 1930’s. The collection has been transported on loan numbers of times, and studied by several specialists. Today, the collection is in only fair condition in terms of quality of preservation and clarity of labelling. Apart from the thorough work of Cynthia Ahearn in the Smithsonian there were very few attempted identification labels in the lots. David Pawson (*pers. comm.*) commented that he noticed that very few lots had labels when he transported the collection from Harvard to Washington. We found that the condition of some specimens was such that we could not identify them. We note again the National Institute of Oceanography



Figure 4. Sea cucumber specialists who contributed to the identifications of the specimen lots that are the subject of this report. a, Elizabeth Deichmann (1896–1975; photo provided by David Pawson in USNM); b, Cynthia (Gust) Ahearn (1952–2008); c, Melanie Mackenzie (Museum Victoria); d, Emily Whitfield (volunteer in Museum Victoria).

reported that Deichmann had “a considerable part of the material packed up and sent over to Harvard”, and Deichmann’s comment that some of the locality data were “somewhat mixed up”. We found some discrepancies between the data on labels in lots and the lists of data in the *Discovery* Reports. We thus have some reservations about the absolute accuracy of what we are reporting here.

The *Terra Nova* (1910–1913) collection was sent to Museum Victoria from the Smithsonian with the *Discovery* collection, and the lots have been identified where possible. This collection and the documentation are in poor condition. The collection currently in Museum Victoria is being prepared for return to the Natural History Museum in London. We are collaborating with Stefano Schiaparelli (*pers. comm.* University of Genova) who is developing a report on the holothuroids of Terra Nova Bay that will incorporate some of the *Terra Nova* collection data. O’Loughlin (2009) published a final report on *The British, Australian and New Zealand Antarctic Research Expedition* holothuroids (BANZARE, 1929–1930). This collection is lodged in the South Australian Museum.

Abbreviations

| | |
|-------|---|
| BAS | British Antarctic Survey |
| D | Station data prefix for RRS <i>Discovery I</i> and <i>II</i> collections |
| MCZ | Museum of Comparative Zoology, Harvard University |
| MS | Station data prefix for the Marine Biological Stations in South Georgia and in South Africa |
| MNHN | Muséum national d’Histoire naturelle, Paris |
| NHMUK | Natural History Museum, London |
| NMV | Museum Victoria, Australia |
| USNM | United States National Museum (part of Smithsonian Institution) |
| WS | Station data prefix for RRS <i>William Scoresby</i> collections |
| ZMUC | Zoological Museum University of Copenhagen |

Methods

The macro images of preserved specimens were taken by Caroline Harding, with Mark O’Loughlin, using a Canon 5D mark ii camera mounted on a camlift Visionary Digital auto stepper, and Zerene Image Stacker, Adobe Lightroom and Photoshop for image processing and editing. The photos of ossicles were taken by Caroline Harding, with Mark O’Loughlin, using a LEICA DM5000 B microscope, Leica application software, and Helicon Focus montage software.

New taxa from the *Discovery* Expedition (1926–1939)

Order **Dendrochirotida** Grube, 1840

Family **Cucumariidae** Ludwig, 1894

Subfamily **Cucumariinae** Ludwig, 1894 *sensu* Panning 1949

Remarks. The subfamily Cucumariinae has plates only in the

body wall, while the second subfamily Colochirinae Panning, 1949 has plates and bowl/cup/basket ossicles in the body wall.

Cucusquama O’Loughlin gen. nov.

Zoobank *LSID.* <http://zoobank.org/urn:lsid:zoobank.org:act:0BE9B60F-195B-4F04-A06A-7EAF0BAA9D44>

Diagnosis. Cucumariid genus; body sub-pentagonal in transverse section, fusiform; tentacles 10, short, lobed; calcareous ring cucumariid-like; complete calcareous body cover of imbricating, single-layered, perforated plates/scales, free ends point posteriorly; tube feet radial only, walls covered with scales; absence of cups and tables.

Type species and locality. *Cucusquama wesafrika* O’Loughlin sp. nov. (equatorial west Africa). Monotypic.

Etymology. Named *Cucu* from the family name Cucumariidae, with recognition of cucumariid like characters, and *squama* from the Latin *squama* (meaning scale) with reference to the body cover of imbricating scales.

Remarks. The sub-pentagonal form, complete body cover of imbricating scales, 10 short lobed tentacles, and radial series of tube feet is a unique combination of morphological characters within family Cucumariidae. We reluctantly establish a new monotypic genus.

Cucusquama wesafrika O’Loughlin sp. nov.

Zoobank *LSID.* <http://zoobank.org/urn:lsid:zoobank.org:act:D4A442DB-36E7-453C-945D-47FA23AB6CAA>

Table 1; figures 5, 6

Material examined. Holotype. West Africa, Luanda, Angola, *Discovery* stn D 274, -8.84 13.23 64–65 m, 4 Aug 1927, NHMUK 2016.148.

Paratypes (4). West Africa, off Cape Lopez, Gambon (French Congo), *Discovery* stn D 279, -0.63 8.70 58–67 m, 10 Aug 1927, NHMUK 2016.149–152.

Description. Body (preserved) up to 13 mm axial length, up to 3 mm high, body form sub-pentagonal, body tapered anteriorly and posteriorly, long posterior taper to create a tail; body completely invested in imbricating scales, free ends of imbricating scales point posteriorly; oral disc at base of oral cavity created by anteriorly-projecting scales; no anal scales detected; 10 short, lobed, black tentacles in ring on oral disc; ring not strongly calcified, form weakly evident, cucumariid-like; internal organs shriveled, brittle; tube feet on radii only, in single spaced series, up to 12 tube feet on any radius, tube feet more strongly developed on mid-ventral and ventro-lateral radii, wall of tube feet covered with imbricating scales.

Body wall ossicles single-layered perforated plates only, irregularly oval; large plates scales up to 600 μ m long; some irregular smaller plates up to about 170 μ m long; no evidence of cups or tables detected. No tube foot endplates detected. No tentacle ossicles detected.

Distribution. Equatorial West Africa, off Angola and Gambon, 58–67 m.

Table 1. Complete list of *Discovery* Expedition taxa collected from 1926 to 1939 (H indicates holotype; P indicates paratype(-s)).

| Taxa (grouped in orders, in alphabetical sequence) | Station number | Locality | Depth | NHMUK registration (+ MNHN, ZMUC) |
|---|----------------|--------------------------------|-----------|-----------------------------------|
| Aspidochirotida | | | | |
| <i>Pseudostichopus spiculiferus</i> (O'Loughlin, 2002) | D 1658 | Ross Sea | 520 m | 2011.169–170 (3) |
| <i>Pseudostichopus spiculiferus</i> (O'Loughlin, 2002) | D 600 | South Shetland Islands | 501–527 m | 2011.297 (1) |
| <i>Pseudostichopus spiculiferus</i> (O'Loughlin, 2002) | D 1660 | Ross Sea | 351 m | 2016.175–177 |
| Dendrochirotida | | | | |
| <i>Amphicyclus thomsoni</i> (Hutton, 1878) | D 941 | Cook Strait, New Zealand | 128 m | 2016.134–135 |
| <i>Cladodactyla crocea</i> (Lesson, 1830) | WS 869 | Falkland Islands | 187 m | 2016.100 |
| <i>Cladodactyla crocea</i> (Lesson, 1830) | WS 231 | Falkland Islands | 159–167 m | 2016.101 |
| <i>Cladodactyla crocea</i> (Lesson, 1830) | WS 867 | Falkland Islands | 147–150 m | 2016.102 |
| <i>Cladodactyla crocea</i> (Lesson, 1830) | WS 804 | Falkland Islands | 143–150 m | 2016.147 |
| 'Clarkiella discoveryi Heding, 1954 (in Heding & Panning, 1954) H | D 474 | W of Shag Rocks, South Georgia | 199 m | ZMUC HOL–64 |
| 'Clarkiella discoveryi Heding, 1954 (in Heding & Panning, 1954) P | D 474 | W of Shag Rocks, South Georgia | 199 m | ZMUC HOL–247 |
| <i>Crucella scotiae</i> (Vaney, 1906) | D 2567 | Haakon VII Sea | 100–124 m | 2011.196 |
| <i>Crucella scotiae</i> (Vaney, 1906) | D 175 | South Shetland Islands | 200 m | 2011.168 |
| <i>Cucamba psolidiformis</i> (Vaney, 1908) | D 1872 | South Shetland Islands | 247 m | 2016.140 |
| <i>Cucamba psolidiformis</i> (Vaney, 1908) | D 1660 | Ross Sea | 351 m | 2016.145 |
| <i>Cucumaria dudexa</i> O'Loughlin & Manjón-Cabeza, 2009b | D 456 | Ross Sea | 40–45 m | 2011.141–150 (16) |
| <i>Cucusquama wesafrika</i> O'Loughlin sp. nov. H | D 274 | off Luanda, Angola | 64–65 m | 2016.148 |
| <i>Cucusquama wesafrika</i> O'Loughlin sp. nov. P | D 279 | Cape Lopez, French Congo | 58–67 m | 2016.149–152 |
| <i>Echinopsolus acanthocola</i> Gutt, 1990 | D 1660 | Ross Sea | 351 m | 2016.141 |
| <i>Echinopsolus acanthocola</i> Gutt, 1990 | D 1660 | Ross Sea | 351 m | 2016.156–161 |
| <i>Echinopsolus acutus</i> (Massin, 1992) | D 1652 | Ross Sea | 567 m | 2011.341 |
| <i>Echinopsolus acutus</i> (Massin, 1992) | D 1872 | South Shetland Islands | 247 m | 2011.342–344 |
| <i>Echinopsolus acutus</i> (Massin, 1992) | D 1652 | Ross Sea | 567 m | 2016.162–170 |
| <i>Echinopsolus attenuatus</i> (Vaney, 1906) | D 1652 | Ross Sea | 567 m | 2011.366 |
| <i>Echinopsolus georgiana</i> (Lampert, 1886) group Gutt, 1988 | D 1652 | Ross Sea | 567 m | 2011.367 |
| <i>Echinopsolus georgiana</i> (Lampert, 1886) group Gutt, 1988 | WS 228 | Falkland Islands | 229–236 m | 2016.154 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | WS 245 | Falkland Islands | 209–304 m | 2016.171–173 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 159 | South Georgia | 160 m | 2011.314–315 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 160 | Shag Rocks | 0–180 m | 2011.316–320 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | WS 33 | South Georgia | 0–130 m | 2011.321 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | WS 33 | South Georgia | 0–130 m | 2011.322 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 156 | South Georgia | 200–236 m | 2011.323 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 148 | South Georgia | 132–148 m | 2011.324 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | WS 840 | Falkland Islands | 368–463 m | 2011.325 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 175 | South Shetland Islands | 200 m | 2011.326 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 363 | South Sandwich Islands | 278–329 m | 2011.327–328 |
| <i>Echinopsolus koehleri</i> (Vaney, 1914) | D 160 | Shag Rocks | 0–180 m | 2011.329–336 |
| <i>Echinopsolus mollis</i> (Ludwig & Heding, 1935) | D 363 | South Sandwich Islands | 278–325 m | 2016.104–107 |
| <i>Hemioedema spectabilis</i> (Ludwig, 1883) | WS 797 | Falkland Islands | 112–114 m | 2016.136 |
| <i>Heterocucumis steineni</i> (Ludwig, 1898) | D 456 | Ross Sea | 40–45 m | 2011.162–167 |
| <i>Heterocucumis steineni</i> (Ludwig, 1898) | D 2567 | Haakon VII Sea | 100–124 m | 2011.197 |

| Taxa (grouped in orders, in alphabetical sequence) | Station number | Locality | Depth | NHMUK registration (+ MNHN, ZMUC) |
|--|--------------------|-------------------------------------|--------------------|-----------------------------------|
| <i>Heterothyone ocnoides</i> (Dendy, 1897) | D 939 | off Dargaville, New Zealand | 87 m | 2016.113–115 |
| <i>Neopsolidium convergens</i> (Hérouard, 1901) | D 724 | Strait of Magellan | 0–5 m | 2011.126–132 |
| <i>Neopsolidium convergens</i> (Hérouard, 1901) | WS 84 | Falkland Islands | 74–75 m | 2011.133 |
| <i>Neopsolidium convergens</i> (Hérouard, 1901) | D 51 | Falkland Islands | 115 m | 2011.134–137 |
| <i>Neopsolidium kerguelensis</i> (Théel, 1886) | D 1564 | Marion Island | 108–113 m | 2016.178 |
| <i>Neothyonidium armatum</i> Pawson, 1965 | D 941 | Cook Strait, New Zealand | 128 m | 2016.153 |
| <i>Ocnus capensis</i> (Théel, 1886) | MS 82 | Saldanha Bay, South Africa | 7–14 m | 2016.143 |
| <i>Paracucumis turricata</i> (Vaney, 1906) | D 1651 | Ross Sea | 594 m | 2011.139–140 |
| <i>Parathyonidium incertum</i> Heding, 1954 (in Heding & Panning, 1954) H | ² D 170 | ² South Shetland Islands | ² 342 m | ³ ZMUC HOL–93 |
| <i>Parathyonidium incertum</i> Heding, 1954 (in Heding & Panning, 1954) P | D 170 | South Shetland Islands | 342 m | ZMUC HOL–300 |
| <i>Parathyonidium incertum</i> Heding, 1954 (in Heding & Panning, 1954) P | D 170 | South Shetland Islands | 342 m | 2011.171–173 |
| <i>Parathyonidium incertum</i> Heding, 1954 (in Heding & Panning, 1954) P | No data | Elephant Island | 600 m | MNHN–IE–2013–2479 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 867 | Falkland Islands | 148–150 m | 2016.116–129 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 84 | Falkland Islands | 74–75 m | 2011.81–90 (23) |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 85 | Falkland Islands | 79 m | 2011.91–99 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 51 | Falkland Islands | 115 m | 2011.100–101 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 804 | Falkland Islands | 143–150 m | 2011.102–110 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 863 | Patagonia Shelf | 117–121 m | 2011.111 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 93 | Falkland Islands | 130–133 m | 2011.112 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 652 | Burdwood Bank | 169–171 m | 2011.113 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 56 | Larsen Harbour, South Georgia | 2 m | 2016.132–133 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 1909 | Falkland Islands | 132 m | 2016.174 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 243 | Falkland Islands | 141–144 m | 2011.114 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 81 | Falkland Islands | 81–82 m | 2011.115 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 80 | Falkland Islands | 152–156 m | 2011.116 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 865 | Patagonia Shelf | 126–128 m | 2011.117 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 804 | Falkland Islands | 143–150 m | 2011.118 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 834 | off Patagonia | 27–38 m | 2011.119 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 65 | Undine Harbour, South Georgia | 1 m (kelp) | 2011.120 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 80 | Falkland Islands | 152–156 m | 2011.121–123 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 52 | Falkland Islands | 17 m | 2011.124 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 216 | Falkland Islands | 133–219 m | 2011.125 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 51 | Falkland Islands | 115 m | 2011.186–192 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 804 | Falkland Islands | 143–150 m | 2011.193 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 56 | Larsen Harbour, South Georgia | 2 m | 2011.194–195 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 724 | Fortesque Bay, Magellan Strait | 0–5 m | 2011.184–185 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 836 | Patagonia Shelf | 64 m | 2011.228 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 247 | Falkland Islands | 172 m | 2011.229 |

| Taxa (grouped in orders, in alphabetical sequence) | Station number | Locality | Depth | NHMUK registration (+ MNHN, ZMUC) |
|--|----------------|--------------------------------|------------|-----------------------------------|
| <i>Pentactella leonina</i> (Semper, 1867) | D 53 | Port Stanley, Falkland Islands | 0–2 m | 2011.230–231 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 55 | Port Stanley, Falkland Islands | 10–16 m | 2011.232–235 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 576 | Falkland Islands | 24–34 m | 2011.236–237 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 249 | Falkland Islands | 166 m | 2011.238 |
| <i>Pentactella leonina</i> (Semper, 1867) | WS 848 | Patagonia Shelf | 115–117 m | 2011.239–240 |
| <i>Pentactella leonina</i> (Semper, 1867) | D 53 | Port Stanley, Falkland Islands | 0–2 m | 2011.241 |
| <i>Pentactella leoninoides</i> (Mortensen, 1925) | D 2215 | NZ Antipodes Island | 163–210 m | 2011.174 |
| <i>Pentactella marionensis</i> (Théel, 1886) | D 1563 | Marion Island | 101–106 m | 2011.221–224 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 867 | Falkland Islands | 148–150 m | 2016.99 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 804 | Falkland Islands | 143–150 m | 2016.146 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 840 | Falkland Islands | 386–463 m | 2011.1 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 246 | Falkland Islands | 208–267 m | 2011.2–5 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | D 51 | Falkland Islands | 115 m | 2011.6–9 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 246 | Falkland Islands | 208–267 m | 2011.10–13 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 65 | Undine Harbour, South Georgia | 1 m (kelp) | 2011.14 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | D 1909 | Falkland Islands | 132 m | 2011.15 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 225 | Falkland Islands | 161–162 m | 2011.16 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | D 388 | Cape Horn | 121 m | 2011.17–21 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 243 | Falkland Islands | 141–144 m | 2011.22–23 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 228 | Falkland Islands | 229–236 m | 2011.24–26 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 840 | Falkland Islands | 368–463 m | 2011.27 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 228 | Falkland Islands | 229–236 m | 2011.28–30 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 73 | Falkland Islands | 121–130 m | 2011.31–33 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 804 | Falkland Islands | 143–150 m | 2011.34–36 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 84 | Falkland Islands | 74–75 m | 2011.37 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 583 | Magellan Strait | 14–78 m | 2011.38–40 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 243 | Falkland Islands | 141–144 m | 2011.41–42 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 237 | Falkland Islands | 150–256 m | 2011.43 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | D 1909 | Falkland Islands | 132 m | 2011.44–46 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 88 | Falkland Islands | 118 m | 2011.47–56 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 246 | Falkland Islands | 208–267 m | 2011.57–59 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 825 | Falkland Islands | 135–144 m | 2011.60–69 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 839 | Falkland Islands | 503–534 m | 2011.70 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 804 | Falkland Islands | 143–150 m | 2011.71 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 825 | Falkland Islands | 135–144 m | 2011.72–75 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 93 | Falkland Islands | 130–133 m | 2011.76–77 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | D 141 | Cumberland Bay, South Georgia | 17–27 m | 2011.78 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 841 | Falkland Islands | 100–110 m | 2011.79 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 231 | Falkland Islands | 159–167 m | 2011.80 |
| <i>Pentactella perrieri</i> (Ekman, 1927) | WS 825 | Falkland Islands | 135–144 m | 2011.198–204 |
| <i>Pentamera chiloensis</i> (Ludwig, 1887) | WS 816 | Patagonia Shelf | 150 m | 2011.227 |
| <i>Pentamera chiloensis</i> (Ludwig, 1887) | WS 71 | Falkland Islands | 80–82 m | 2011.225–226 |
| <i>Pseudocnella insolens</i> (Théel, 1886) | MS 82 | Saldanha Bay, South Africa | 7–14 m | 2011.284–293 (10+) |

| Taxa (grouped in orders, in alphabetical sequence) | Station number | Locality | Depth | NHMUK registration (+ MNHN, ZMUC) |
|---|----------------|--------------------------------|-----------|-----------------------------------|
| <i>Psolocrux coatsi</i> (Vaney, 1908) | WS 56 | Larsen Harbour, South Georgia | 2 m | 2011.151–152 |
| <i>Psolocrux juvenilesi</i> O'Loughlin & Manjón-Cabeza, 2009b | D 363 | South Sandwich Islands | 278–329 m | 2011.153 |
| <i>Psolocrux juvenilesi</i> O'Loughlin & Manjón-Cabeza, 2009b | D 159 | South Georgia | 160 m | 2011.313 |
| <i>Psolidium dorsipes</i> Ludwig, 1887 | WS 834 | Cape Virgenes, Argentina | 27–38 m | 2008.3182 |
| <i>Psolidium gaini</i> Vaney, 1914 | D 1660 | Pennell Bank, Ross Sea | 0–351 m | 2008.3183–3189 |
| <i>Psolidium incubans</i> Ekman, 1925 | MS 67 | Cumberland Bay, South Georgia | 38 m | 2008.3190 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 181 | Palmer Archipelago | 160–335 m | 2008.3191 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 182 | Palmer Archipelago | 278–500 m | 2008.3192 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 187 | Palmer Archipelago | 0–195 m | 2008.3193 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 190 | Palmer Archipelago | 0–250 m | 2008.3194–3196 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 599 | Antarctic Peninsula | 0–150 m | 2008.3197–3198 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1644 | Ross Sea | 626 m | 2008.3199 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1649 | Ross Sea | 695 m | 2008.3200–3201 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1652 | Ross Sea | 567 m | 2008.3202–3205 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1660 | Ross Sea | 0–351 m | 2008.3206–3208 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 2200 | Balleny Islands | 512–532 m | 2008.3209–3218 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | D 55 | Port Stanley, Falkland Islands | 10–16 m | 2016.69–74 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | D 1909 | Burdwood Bank | 132 m | 2016.75 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | D 1909 | Burdwood Bank | 132 m | 2011.345–354 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | D 1909 | Burdwood Bank | 132 m | 2011.355 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | WS 804 | Falkland Islands | 143–150 m | 2016.76 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | WS 243 | Falkland Islands | 141–144 m | 2016.77 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | WS 825 | Falkland Islands | 135–144 m | 2016.78–80 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | WS 244 | Falkland Islands | 253–247 m | 2016.81 |
| <i>Psolus antarcticus</i> (Philippi, 1857) | D 2200 | Balleny Islands | 512–532 m | 2016.82 |
| <i>Psolus carolineae</i> O'Loughlin & Whitfield, 2010 | D 1952 | South Shetland Islands | 367–383 m | 2016.108–110 |
| <i>Psolus dubiosus</i> Ludwig & Heding, 1935 | D 1652 | Ross Sea | 567 m | 2016.84–88 |
| <i>Psolus dubiosus</i> Ludwig & Heding, 1935 | D 1660 | Ross Sea | 351 m | 2016.89–90 |
| <i>Psolus dubiosus</i> Ludwig & Heding, 1935 | D 1652 | Ross Sea | 567 m | 2016.91–92 |
| <i>Psolus dubiosus</i> Ludwig & Heding, 1935 | D 474 | West of Shag Rocks | 199 m | 2016.93–98 |
| <i>Psolus figulus</i> Ekman, 1925 | MS 67 | Cumberland Bay, South Georgia | 38 m | 2016.43 |
| <i>Psolus figulus</i> Ekman, 1925 | WS 56 | Larsen Harbour, South Georgia | 2 m | 2016.44–46 |
| <i>Psolus lockhartae</i> O'Loughlin & Whitfield, 2010 | WS 840 | Falkland Islands | 368–463 m | 2016.83 |
| <i>Psolus paradubiosus</i> Carriol & Féral, 1985 | D 1563 | Marion Island | 99–113 m | 2016.111–112 |
| <i>Psolus patagonicus</i> Ekman, 1925 | D 175 | South Shetland Islands | 200 m | 2016.130 |
| <i>Psolus patagonicus</i> Ekman, 1925 | D 1957 | South Shetland Islands | 785–810 m | 2016.131 |
| <i>Psolus patagonicus</i> Ekman, 1925 | WS 56 | East Falklands | 10–16 m | 2011.376–377 |
| <i>Psolus patagonicus</i> Ekman, 1925 | WS 85 | Falkland Islands | 79 m | 2011.356–365 |
| <i>Psolus patagonicus</i> Ekman, 1925 | D 1909 | Falkland Islands | 132 m | 2011.369–371 |
| <i>Psolus patagonicus</i> Ekman, 1925 | WS 848 | Patagonia Shelf | 115–117 m | 2011.372 |
| <i>Psolus patagonicus</i> Ekman, 1925 | D 724 | Strait of Magellan | 0–5 m | 2011.373 |

| Taxa (grouped in orders, in alphabetical sequence) | Station number | Locality | Depth | NHMUK registration (+ MNHN, ZMUC) |
|---|----------------|-------------------------------|-----------|-----------------------------------|
| <i>Psolus patagonicus</i> Ekman, 1925 | WS 243 | Falkland Islands | 141–144 m | 2011.374 |
| <i>Psolus patagonicus</i> Ekman, 1925 | WS 841 | Falkland Islands | 100–110 m | 2011.375 |
| <i>Psolus patagonicus</i> Ekman, 1925 | WS 820 | Falkland Islands | 351–368 m | 2011.378 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 148 | South Georgia | 132–148 m | 2016.1–24 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 474 | West of Shag Rocks | 199 m | 2016.25 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 140 | South Georgia | 122–136 m | 2016.26–27 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 27 | South Georgia | 110 m | 2016.28 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 179 | Palmer Archipelago | 4–10 m | 2016.29–32 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 42 | Cumberland Bay, South Georgia | 120–204 m | 2016.33–39 |
| <i>Psolus punctatus</i> Ekman, 1925 | D 190 | Palmer Archipelago | 130 m | 2016.40–42 |
| <i>Staurocucumis liouvillei</i> (Vaney, 1914) | D 456 | Ross Sea | 40–45 m | 2016.137–139 |
| <i>Staurocucumis liouvillei</i> (Vaney, 1914) | WS 225 | Falkland Islands | 161–162 m | 2016.155 |
| <i>Staurocucumis liouvillei</i> (Vaney, 1914) | D 140 | South Georgia | 122–136 m | 2011.159–161 |
| <i>Staurocucumis liouvillei</i> (Vaney, 1914) | D 366 | South Sandwich Islands | 77–152 m | 2011.154–158 |
| <i>Staurocucumis liouvillei</i> (Vaney, 1914) | D 123 | South Georgia | 230–250 m | 2011.340 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 27 | Cumberland Bay, South Georgia | 110 m | 2016.142 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 144 | South Georgia | 155–178 m | 2011.175 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 160 | Shag Rocks | 0–180 m | 2011.176–177 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 1652 | Ross Sea | 567 m | 2011.178 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 170 | South Shetland Islands | 342 m | 2011.179–180 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 1660 | Ross Sea | 351 m | 2011.181–182 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 1658 | Ross Sea | 520 m | 2011.183 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | WS 71 | Falkland Islands | 80–82 m | 2011.337–338 |
| <i>Trachythone bouvetensis</i> (Ludwig & Heding, 1935) | D 42 | Cumberland Bay, South Georgia | 120–204 m | 2011.339 |
| <i>Trachythone parva</i> (Ludwig, 1875) | WS 795 | Falkland Islands | 157–161 m | 2016.103 |
| <i>Thyone aurea</i> (Quoy & Gaimard, 1834) | MS 82 | Saldanha Bay, South Africa | 7–14 m | 2011.294–296 |
| Elasipodida | | | | |
| <i>Peniagone vignoni</i> Hérouard, 1901 | D 181 | Palmer Archipelago | 160–335 m | 2011.311–312 |
| <i>Rhipidothuria racovitzae</i> Hérouard, 1901 | D 181 | Palmer Archipelago | 160–335 m | 2011.298–307 (20) |
| <i>Rhipidothuria racovitzae</i> Hérouard, 1901 | D 1952 | South Shetland Islands | 367–383 m | 2011.308–310 |
| Synaptida (sensu Smirnov 2012) | | | | |
| <i>Chiridota pisanii</i> Ludwig, 1887 | WS 750 | off Patagonia | 95 m | 2010.110 |
| <i>Chiridota pisanii</i> Ludwig, 1887 | WS 388 | Cape Horn | 121 m | 2010.111 |
| <i>Paradota weddellensis</i> Gutt, 1990 | WS 217 | Falkland Islands | 146 m | 2011.242 |
| <i>Paradota weddellensis</i> Gutt, 1990 | D 600 | South Shetland Islands | 501–527 m | 2011.243 |
| <i>Scoliorhapis massini</i> O’Loughlin & VandenSpiegel, 2010 | WS 756 | Falkland Islands | 119 m | 2010.105–109 |
| <i>Scoliorhapis massini</i> O’Loughlin & VandenSpiegel, 2010 (“probably”) | MS 67 | Cumberland Bay, South Georgia | 38 m | 2010.112–113 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 816 | Patagonia Shelf | 150 m | 2010.55–62 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 88 | Falkland Islands | 118 m | 2010.63–68 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 84 | Falkland Islands | 75 m | 2010.69–70 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 773 | Falkland Islands | 296 m | 2010.71–74 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 82 | Falkland Islands | 140–144 m | 2010.75–84 |

| Taxa (grouped in orders, in alphabetical sequence) | Station number | Locality | Depth | NHMUK registration (+ MNHN, ZMUC) |
|---|----------------|-------------------------------|-----------|-----------------------------------|
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 25 | Undine Harbour, South Georgia | 18–27 m | 2010.85–94 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 56 | Larsen Harbour, South Georgia | 2 m | 2010.95–96 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 39 | Cumberland Bay, South Georgia | 179–235 m | 2010.97–98 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 126 | South Georgia | 0–100 m | 2010.99 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 62 | Wilson Harbour, South Georgia | 15–45 m | 2010.100–103 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 1941 | South Georgia | 22–25 m | 2010.104 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 1562 | Marion Island | 88–104 m | 2016.47–68 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 83 | Falkland Islands | 129–137 m | 2011.138 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 804 | Falkland Islands | 143–150 m | 2011.205–211 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 228 | Falkland Islands | 229–236 m | 2011.212–220 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 869 | Patagonia Shelf | 187 m | 2011.244–253 (50+) |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 45 | South Georgia | 238–270 m | 2011.254–263 (20+) |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 145 | South Georgia | 26–35 m | 2011.264–273 (10+) |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 838 | Patagonia Shelf | 149–159 m | 2011.274–283 (10+) |
| ⁴ <i>Sigmodota magnibacula</i> (Massin & Hétier, 2004) | ? | ? | ? | 2016.144 |
| taeniogyrinid species (very poor condition) | WS 182 | Palmer Archipelago | 278–500 m | 2010.114 |

¹See note 1 with Table 2 below.

²See note 2 with Table 2 below.

³Holotype specimen is thought to be lost. See note 3 with Table 2 below.

⁴Specimen and locality source not recognized. May not be *Discovery* Expedition. Handwritten label with: St. 105, 13/2/'31, 163 m.

Etymology. Named *wesafrika* for the geographical occurrence of the species on the West Africa coast.

Remarks. All the type specimens have dried during preservation, and the calcareous ring and ossicles are partly at least eroded. The ring does not have a recognizable outline in any specimen that was dissected. The form and number of the tentacles are difficult to observe. The sub-pentagonal form, complete body cover of imbricating scales with free ends pointing posteriorly, 10 short lobed tentacles, radial series of tube feet, and absence of cups or tables distinguish the new genus and species.

Previous publications with *Discovery* Expedition Holothuroidea (included in Table 1 and listed in Tables 2, 3, 4).

1. Albert Panning (in Heding & Panning 1954) recorded that Svend Heding died (in 1949) before their manuscript was completed, and before Heding was able to complete any *Discovery* Expedition Report. Panning acknowledged that descriptions of the new genera and species *Clarkiella* Heding, 1954, *Clarkiella discoveryi* Heding, 1954, *Parathyonidium* Heding, 1954 and *Parathyonidium incertum* Heding, 1954 were from the notes of Heding. In collaboration with Elizabeth Deichmann (at the MCZ at Harvard University at the time) Panning included these new taxa in the comprehensive paper

Heding & Panning 1954. Panning (in Heding & Panning 1954) recorded that the work on the *Discovery* material was taken over by Dr. Deichmann. This was not completed, and no *Discovery* Report has been published.

O'Loughlin (2009), in a paper on the BANZARE holothuroids, discussed *Clarkiella* Heding, and referred a new holothuroid species from the Kerguelen Islands and Tasmania to Heding's genus: *Clarkiella deichmannae* O'Loughlin, 2009.

O'Loughlin *et al.* (2009a), in reporting some observations of reproductive strategies of dendrochirotid species, referred to an as then undescribed species of *Parathyonidium* Heding from Eastern Antarctica that exhibited brood-protection in the coelom. Subsequently O'Loughlin *et al.* (2014) included an illustrated revision of genus *Parathyonidium* Heding and species *Parathyonidium incertum* Heding. Their revision was based on the original description and on three paratypes from the South Shetland Islands. Additional specimens were recognized from South Georgia, from the Antarctic Peninsula, and off Enderby Land in Eastern Antarctica. The specimen referred to *Parathyonidium* by O'Loughlin *et al.* (2009a) was identified as *P. incertum*. ZMUC records (see note 3 under Table 2) indicate that the holotype for *Parathyonidium incertum* "must probably be considered lost". O'Loughlin *et al.* (2014) listed three lots of paratypes that are held respectively in Copenhagen (ZMUC), Paris (MNHN) and London

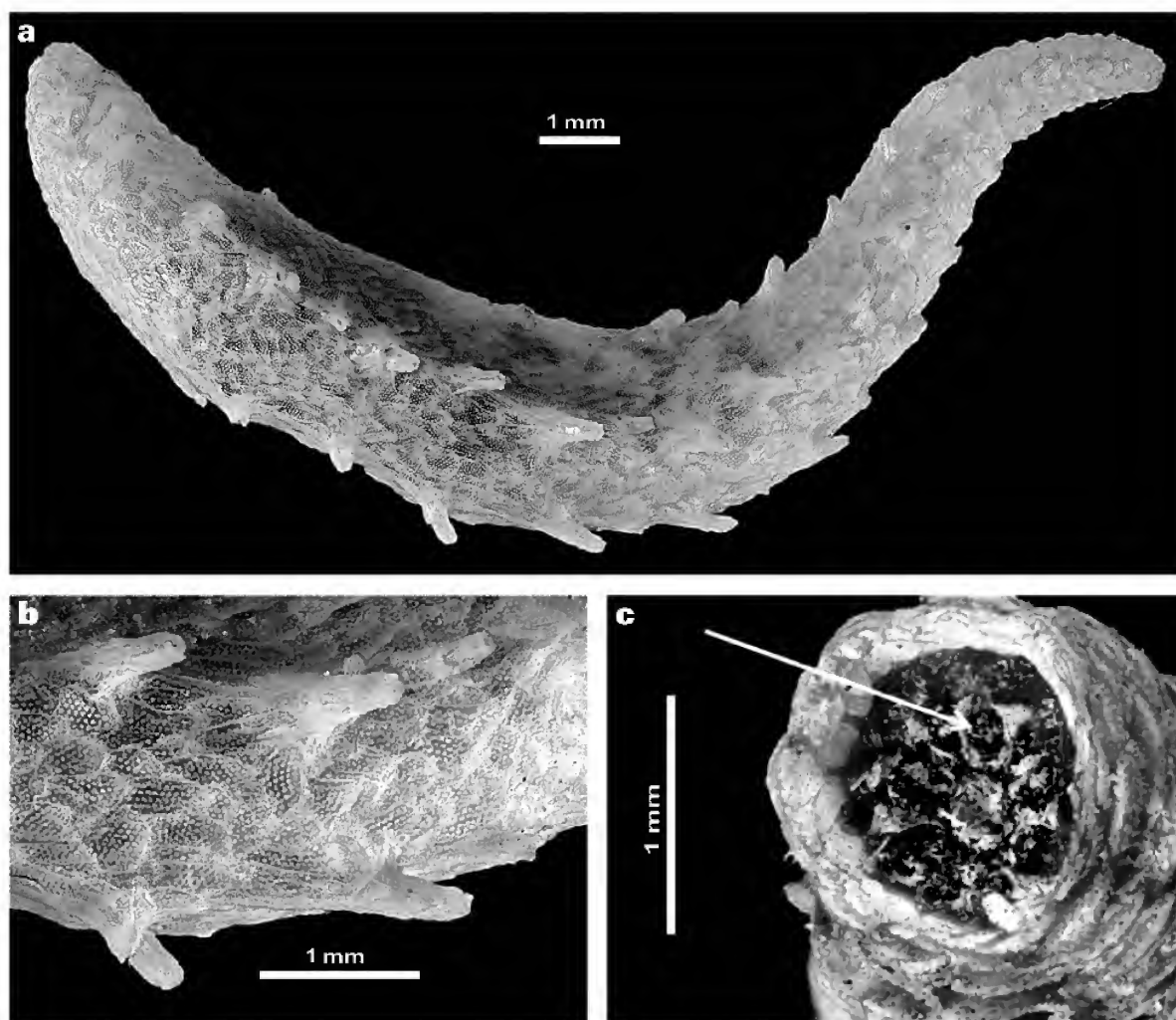


Figure 5. a & b, photos of preserved holotype of *Cucusquama wesafrika* O'Loughlin gen. & sp. nov. from Angola (oral end left; axial length 13 mm; NHMUK 2016.148); c, photo into mouth cavity of a preserved paratype from Gambon (French Congo) (arrow pointing to one black tentacle; NHMUK 2016.149).

(NHMUK). Details are provided in Tables 1 & 2. O'Loughlin *et al.* (2014) reported the holotype locality for *Parathyonidium incertum* as Shag Rocks near South Georgia, based on Heding & Panning (1954). We judge here that this was a mistake (see note 2 with Table 2 below).

2. O'Loughlin & Ahearn (2008) reported 13 lots of *Discovery* Expedition holothuroids that represent four species of *Psolidium* Ludwig, 1875. Details are provided in Tables 1 and 3.

3. O'Loughlin & VandenSpiegel (2010) reported 16 lots of *Discovery* Expedition Synaptida (as Apodida) holothuroids that represented 3 species. Details are provided in Tables 1 and 4.

Systematic notes on *Discovery* holothuroid taxa.

1. *Echinopsolus* Gutt, 1990.

Bohn & Hess (2014) reassigned a group of Antarctic cucumariid species to genus *Echinopsolus* Gutt, 1990, based on their shared and unique set of morphological characters related to their reproductive mode. The group comprised: *Echinopsolus acanthocola* Gutt, 1990; *E. acutus* (Massin, 1992); *E. charcoti* (Vaney, 1906); *E. koehleri* (Vaney, 1914); *E. mollis* (Ludwig & Heding, 1935); *E. parvipes* (Massin, 1992); *E. splendidus* (Gutt, 1990). In the same paper Bohn & Hess (2014) reassigned genus *Echinopsolus* to family Cucumariidae.

Table 2. Type specimens of *Discovery* Expedition Holothuroidea published in Heding & Panning 1954.

| Taxon | Type status | Station collected | Locality collected | Depth | Date collected | Institution lodged | Registration |
|---|-------------------------|----------------------------|---------------------------------------|-------|----------------|--------------------|-------------------------|
| <i>Clarkiella discoveryi</i> Heding (in Heding & Panning, 1954) | ¹ Holotype | D 474 | W of Shag Rocks South Georgia | 199 m | 19 Nov 1930 | ZMUC | HOL-000064 |
| <i>Clarkiella discoveryi</i> Heding, 1954 | ¹ Paratype | D 474 | W of Shag Rocks South Georgia | 199 m | 19 Nov 1930 | ZMUC | HOL-000247 |
| <i>Parathyonidium incertum</i> Heding (in Heding & Panning, 1954) | ^{2,3} Holotype | ³ Lost specimen | | | | | ³ HOL-000093 |
| <i>Parathyonidium incertum</i> Heding, 1954 | Paratypes (3) | D 170 | Clarence Island S Shetland Islands | 342 m | 23 Feb 1927 | ZMUC | HOL-000300 |
| <i>Parathyonidium incertum</i> Heding, 1954 | Paratypes (3) | D 170 | Clarence Island | 342 m | 23 Feb 1927 | NHMUK | NHMUK 2011.171-173 |
| <i>Parathyonidium incertum</i> Heding, 1954 | Partypes (2) | No record | Elephant Island | 600 m | No record | MNHN | MNHN-IE-2013-2479 |

¹No *Discovery* station data were reported for *Clarkiella discoveryi* with the description of the new taxa in Heding & Panning 1954, but registered and labelled holotype and paratype (one) specimens are in the ZMUC with type status, station number and collection data (see Table 2 above with station data from the labels with the types in the ZMUC). Both type specimens were collected from the same type locality, station D474.

² The station data reported for the type for *Parathyonidium incertum* in Heding & Panning (1954) is station D474. We judge that this may be a mistake since it is the type locality on the labels for *Clarkiella discoveryi*. The holotype specimen is assumed to be lost as no “holotype” has been found. But there are paratypes from station D170, and a note on the label with them translated by Tom Schioette in 2013 reads: “Does the identification with them include also the large specimens? Heding’s serial number 234–236 st. 170”. With some reservation we judge that the holotype was most probably also from the paratype station D170, and not station D474 as published in Heding & Panning (1954).

³ Note by Tom Schioette in 2013: “The holotype of *Parathyonidium incertum*, which should probably have been (or perhaps was) returned with the “Discovery” material after Heding’s death, was later given the ZMUC number HOL-93 in absentia. It must probably be considered lost, since later workers on the material have not succeeded in finding it”.

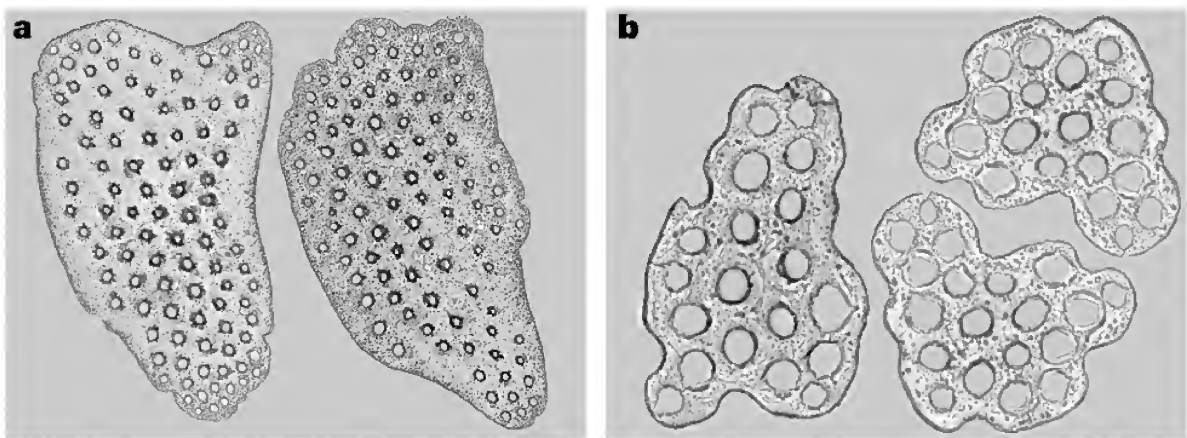


Figure 6. Photos of eroding ossicles from the mid-body wall of *Cucusquama wesafrika* O'Loughlin gen. & sp. nov. a, large single-layered perforated plates (scales) from the holotype (up to 600 μ m long; NHMUK 2016.148); b, body wall and tube foot small perforated plates from a paratype (up to 168 μ m long; NHMUK 2016.150).

Table 3. *Discovery* Expedition Holothuroidea published in O'Loughlin & Ahearn 2008.

| Taxon | Station collected | Locality collected | Depth | Institution lodged | Registration |
|--|-------------------|---|-----------|--------------------|----------------|
| <i>Psolidium dorsipes</i> Ludwig, 1887 | WS 834 | Cape Virgenes Southern Argentina | 27–38 m | NHMUK | 2008.3182 |
| <i>Psolidium gaini</i> Vaney, 1914 | D 1660 | Pennell Bank Ross Sea | 0–351 m | NHMUK | 2008.3183–3189 |
| <i>Psolidium incubans</i> Ekman, 1925 | MS 67 | South Georgia | 38 m | NHMUK | 2008.3190 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 181 | Palmer Archipelago Antarctica | 160–335 m | NHMUK | 2008.3191 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 182 | Palmer Archipelago Antarctica | 278–500 m | NHMUK | 2008.3192 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 187 | Palmer Archipelago Antarctica | 0–195 m | NHMUK | 2008.3193 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 190 | Palmer Archipelago Antarctica | 0–250 m | NHMUK | 2008.3194–3196 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 599 | W of Adelaide Island Antarctic Peninsula | 0–150 m | NHMUK | 2008.3197–3198 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1644 | Ross Sea | 626 m | NHMUK | 2008.3199 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1649 | Ross Sea | 695 m | NHMUK | 2008.3200–3201 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1652 | Ross Sea | 0–500 m | NHMUK | 2008.3202–3205 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 1660 | Ross Sea | 0–351 m | NHMUK | 2008.3206–3208 |
| <i>Psolidium tenue</i> Mortensen, 1925 | D 2200 | Balleny Island Antarctica | 512–532 m | NHMUK | 2008.3209–3218 |

Table 4. *Discovery* Expedition Holothuroidea published in O'Loughlin & VandenSpiegel 2010.

| Taxon | Station collected | Locality collected | Depth | Institution lodged | Registration number |
|---|-------------------|----------------------------|-----------|--------------------|---------------------|
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 816 | Falkland Islands | 150 m | NHMUK | 2010.55–62 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 88 | Falkland Islands | 118 m | NHMUK | 2010.63–68 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 84 | Falkland Islands | 75 m | NHMUK | 2010.69–70 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 773 | Falkland Islands | 296 m | NHMUK | 2010.71–74 |
| ¹ <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 82 | Falkland Islands | 140–144 m | NHMUK | 2010.75–84 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 25 | South Georgia | 18–27 m | NHMUK | 2010.85–94 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 56 | South Georgia | 2 m | NHMUK | 2010.95–96 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 39 | South Georgia | 179–235 m | NHMUK | 2010.97–98 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D126 | South Georgia | 0–100 m | NHMUK | 2010.99 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | WS 62 | South Georgia | 15–45 m | NHMUK | 2010.100–103 |
| <i>Sigmodota contorta</i> (Ludwig, 1875) | D 1941 | South Georgia | 22–55 m | NHMUK | 2010.104 |
| <i>Scoliorhapis massini</i> O'Loughlin & VandenSpiegel, 2010 | WS 756 | Falkland Islands | 119 m | NHMUK | 2010.105–109 |
| <i>Chiridota pisanii</i> Ludwig, 1887 | WS 750 | Patagonia | 95 m | NHMUK | 2010.110 |
| <i>Chiridota pisanii</i> Ludwig, 1887 | WS 388 | Cape Horn South America | 121 m | NHMUK | 2010.111 |

¹See Systematic note 6 below. This entry has been changed from the O'Loughlin & VandenSpiegel 2010 paper.

O'Loughlin *et al.* (2009a) discussed the “*Cucumaria georgiana* (Lampert, 1886) group” of Antarctic species that was created by Gutt (1988), and followed by Massin (1992). O'Loughlin *et al.* (2009a) listed 11 species in this “group”: *Cucumaria acuta* Massin, 1992; *Cucumaria analis* Vaney, 1908; *Cucumaria aspera* Vaney, 1908; *Cucumaria attenuata* Vaney, 1906; *Cucumaria georgiana* (Lampert, 1886); *Cucumaria joubini* Vaney, 1914; *Cucumaria lateralis* Vaney, 1906; *Cucumaria perfida* Vaney, 1908; *Cucumaria periprocta* Vaney, 1908; *Cucumaria secunda* Vaney, 1908; *Cucumaria vaneysi* Cherbonnier, 1949. Bohn & Hess (2014) also discussed this “group”, and we agree that the systematic status of the species in this group requires resolution. Foundational to this systematic resolution must be an establishment of the systematic status of *Cucumaria georgiana* (Lampert, 1886). Bohn & Hess (2014) did not assign the “group” to *Echinopsolus*. We have assigned some *Discovery* Expedition lots to this “group”. Based on the general similarity of their reproductive morphological features with those of the *Echinopsolus* species we have also assigned this “group” to *Echinopsolus*.

Bohn & Hess (2014) were not able to confirm the systematic status of *Echinopsolus excretiospinosus* Massin, 2010, but noted that no brood pouches were reported and the ventral tentacle pair were apparently not smaller than the other tentacles.

COI genetic data (Gustav Paulay *pers. comm.*; see phylogenetic tree in O'Loughlin *et al.* 2011) support a generic clade that includes *Echinopsolus acanthocola* (with apparently two or three cryptic species with geographic congruence), the “*georgiana* group” (with apparently two or three cryptic species with geographic congruence), and the reassigned *Echinopsolus mollis* (apparently two or three cryptic species with geographic congruence). Generic data thus support in part the work of Bohn & Hess (2014). We note that these species also have mid-body dorsal papillae or tube feet, and lack cup (bowl) ossicles in the body wall.

But COI genetic data (Gustav Paulay *pers. comm.*; see phylogenetic tree in O'Loughlin *et al.* 2011) support a generic clade for *Psolus koehleri* and *Psolus charcoti* that is separate from the *Echinopsolus* clade and do not support the reassignment of these two species to *Echinopsolus*. We note that these two species lack mid-body dorsal tube feet or papillae, and do have cup (bowl) ossicles in the body wall. Genetic data to date do not support their assignment to a *Psolus* Oken, 1815 clade. We leave these two species in their current reassignment to *Echinopsolus* until a necessary reassessment of dendrochirotid generic assignments is supported by additional genetic data.

We do not have a COI sequence for the recently reassigned *Echinopsolus splendidus*. This species lacks dorsal and lateral tube feet / papillae, but also lacks cups / bowls in the body wall. It falls morphologically into neither *Echinopsolus* genetic /generic clade. We judge that it will probably fall into another generic clade but in the absence of supportive genetic data we do not change the current reassignment to *Echinopsolus*.

2. *Ocnus capensis* (Théel, 1886).

We have identified a single *Discovery* Expedition specimen from the sub-littoral of Saldanha Bay in south-west South Africa as *Ocnus capensis* (Théel, 1886) (MS 82, off Salamander Point, 7–14 m, 6 Sept 1926, NHMUK 2016.143). We based our determination on the description and illustration by Théel (1886) of the three type specimens collected from 179–274 meters off Cape Town in South Africa. Saldanha Bay is close to the type locality for this species. Based on our laboratory notes and sketches, Frank Rowe (*pers. comm.*) judged that the species is *Ocnus capensis*, but thought that the species would be better assigned to *Pseudocnus* Panning, 1949. Rowe judged that genus *Ocnus* Forbes & Goodsir, 1839 (in Forbes, 1841) is restricted to the Mediterranean and north European shore, and that genus *Pentacta* Goldfuss, 1820 is a monotypic endemic South Africa genus. Thandar (1991) described and illustrated and discussed *Ocnus capensis*, and Ahmed Thandar (*pers. comm.*) expressed some doubt about our identification. He considered the species to be a deep water one. We acknowledge that there is thus some doubt about our identification.

3. *Pentactella* Verrill, 1876.

Many *Discovery* Expedition lots have been identified as species of *Pentactella* Verrill, 1876. Based on morphological characters and distribution consideration, and with the support of some genetic data, O'Loughlin *et al.* (2014) reassigned numbers of species of *Pseudocnus* Panning, 1949 to a new genus *Laevocnus* O'Loughlin (in O'Loughlin *et al.* 2014). Immediately after publication the authors recognized that the type species for the new genus *Laevocnus* was the type species for the monotypic *Pentactella* Verrill, 1876. *Laevocnus* is an objective junior synonym of *Pentactella*. A detailed systematic history of genus *Pentactella*, and the assigned species, is provided by O'Loughlin *et al.* (2015).

4. *Psolus dubiosus* Ludwig & Heding, 1935

COI phylogenetic data (Gustav Paulay *pers. comm.*) strongly support a synonymy for *Psolus arnaudi* Cherbonnier, 1974 and *Psolus cherbonnieri* Carriol & Féral, 1985 with *Psolus dubiosus* Ludwig & Heding, 1935. For *Discovery* Expedition specimens we have not attempted to distinguish the former from *Psolus dubiosus*.

5. *Psolus lockhartae* O'Loughlin & Whitfield, 2010.

We have identified a single specimen from deep water off the Falkland Islands as *Psolus lockhartae* O'Loughlin & Whitfield, 2010 (WS 840, S of Falkland Islands, 368–463 m, 6 Feb 1932, NHMUK 2016.83). The distribution of *Psolus lockhartae* was given by O'Loughlin & Whitfield (2010) as Birdwood Bank, South Georgia, South Shetlands and South Orkneys (211–2897 m). The 12 mm long specimen is smaller than the types (up to 20 mm long). The ossicle complement is the same, and the form of the ossicles is similar but the ossicles in the types are larger. We thus have some reservation over our determination.

6. *Sigmodota contorta* (Ludwig, 1875).

O'Loughlin & VandenSpiegel (2010) published the determinations of numbers of *Discovery* Expedition synaptid (as apodid) holothuroids (see Table 4 above). They reported 10 specimens of *Sigmodota contorta* (Ludwig, 1875) (NHMUK 2010.75–84) from Marine Station 82 (Saldanha Bay). The location of Saldanha Bay in South Africa was not noticed, and the locality was mistakenly given as the Falkland Islands. There have been no other reports of *Sigmodota contorta* from South Africa, and this report for Saldanha Bay is now judged to be a mistake. There is also an RRS *William Scoresby* station 82 and this is now judged to be the source of the specimens. This station WS 82 was off the Falkland Islands at 140–144 m.

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Suction feeding preceded filtering in baleen whale evolution

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Abstract

Marx F.G., Hocking D.P., Park T., Ziegler T., Evans A.R. and Fitzgerald, E.M.G. 2016. Suction feeding preceded filtering in baleen whale evolution. *Memoirs of Museum Victoria* 75: 71–82.

The origin of baleen, the key adaptation of modern whales (Mysticeti), marks a profound yet poorly understood transition in vertebrate evolution, triggering the rise of the largest animals on Earth. Baleen is thought to have appeared in archaic tooth-bearing mysticetes during a transitional phase that combined raptorial feeding with incipient bulk filtering. Here we show that tooth wear in a new Late Oligocene mysticete belonging to the putatively transitional family Aetiocetidae is inconsistent with the presence of baleen, and instead indicative of suction feeding. Our findings suggest that baleen arose much closer to the origin of toothless mysticete whales than previously thought. In addition, they suggest an entirely new evolutionary scenario in which the transition from raptorial to baleen-assisted filter feeding was mediated by suction, thereby avoiding the problem of functional interference between teeth and the baleen rack.

Keywords

Mysticeti; baleen whale; filter feeding; suction feeding; tooth wear; Aetiocetidae

Introduction

Baleen whales (Mysticeti) are the largest animals on Earth and owe their success to baleen, a unique feeding structure allowing them to filter vast quantities of small prey from seawater (Pivovarov, 1979; Werth, 2000b). The baleen apparatus of extant mysticetes consists of a series of keratinous plates suspended from the upper jaw, traditionally thought to be derived from the horny palatal ridges of extant artiodactyls (Werth, 2000b). More recent anatomical work, however, has shown that the basal tissue giving rise to baleen is innervated by the superior alveolar nerves, and is thus more likely homologous with the gingiva (Sawamura, 2008).

Baleen rarely fossilises (Esperante et al., 2008; Gioncada et al., 2016), but is thought to have originated early in mysticete evolution, during a transitional phase combining tooth-based raptorial feeding and baleen-assisted filtering (Deméré and Berta, 2008; Deméré et al., 2008). This transition is seemingly exemplified by the Aetiocetidae – a mostly Oligocene (34–23 Ma) family of archaic mysticetes which retained functional teeth alongside features commonly associated with filter feeding (Deméré et al., 2008). The underlying drivers, mechanics and accuracy of this scenario, however, remain contentious (Fitzgerald, 2010; Marx et al., 2015). Here we show that a new Late Oligocene aetiocetid fossil from

Washington, USA, has a highly distinctive tooth wear pattern that is inconsistent with the presence of baleen, suggesting that this key mysticete adaptation emerged later and much closer to the origin of modern whales than previously thought. Our new fossil displays functional adaptations for suction feeding rather than filtering, casting doubt on the accepted ecomorphological context of chaemysticete evolution. Based on this new information, we re-examine previous arguments in favour of a direct transition from raptorial to filter feeding, and propose an alternative model of baleen evolution more consistent with available evidence both from extant taxa and the fossil record.

Material and Methods

Except for the right p3, the teeth were found encased in soft sediment and washed out using water, with no mechanical or chemical preparation. The remainder of the specimen was prepared mechanically and using 10% acetic acid. All parts of the specimen in figs 1–3 were coated with ammonium chloride prior to photography. Where appropriate, photographs of the specimen were taken at varying foci and digitally stacked in Photoshop CS6. To visualise the gross wear features further, we scanned the two best-preserved teeth via micro-computed tomography using a Zeiss Xradia 520 Versa (Oberkochen,

Germany) at the Monash University X-ray Microscopy Facility for Imaging Geomaterials (XMFIG). The specimens were scanned with a source voltage of 140 kV and current of 70 μ A, an exposure time of 2 seconds per image and a pixel size of 12.7 μ m. 3D surface models were generated in Avizo v9.0.0 (Visualization Science Group) and are available as supplementary 3D figures (figs S1–S2).

Institutional abbreviations

AMP, Ashoro Museum of Paleontology, Ashoro, Hokkaido, Japan; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; NMV, Museum Victoria, Melbourne, Australia; UCMP, University of California Museum of Paleontology, Berkeley, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UWBM, Burke Museum of Natural History and Culture, University of Washington, Seattle, USA.

Results

Description of NMV P252567

The new fossil specimen (NMV P252567) comes from the upper part of the Pysht Formation (Clallam County, Washington State, USA; Late Oligocene) (Prothero et al., 2001), and comprises much of the cranium, both mandibles, and postcranial elements. Overall, the morphology of the skull is intermediate between that of *Aetiocetus* and *Fucaia* (Barnes et al., 1995). A detailed systematic analysis of NMV P252567 is currently under preparation, but it is confidently assigned to Aetiocetidae based on the presence of (i) an enlarged lacrimal incising into the lateral border of the ascending process of the maxilla (Deméré and Berta, 2008; Marx et al., 2015); (ii) a laterally expanded premaxilla overhanging the adjacent portion of the maxilla (Barnes et al., 1995; Fitzgerald, 2010; Geisler and Sanders, 2003; Marx, 2011); (iii) a proportionally large, anterolaterally directed orbit (also present in Mammalodontidae) (Marx, 2011); (iv) a (presumably ligamentous) mandibular symphysis with attendant symphyseal groove (also present in chaemysticetes) (Fitzgerald, 2012); (v) gracile cheek teeth with fused roots (Deméré and Berta, 2008; Marx et al., 2015); and (vi) lingually ornamented tooth crowns (Deméré and Berta, 2008; Marx et al., 2015) (figs 1–3).

Based on the right mandible, NMV P252567 has 11 lower teeth, similar to archaeocetes, mammalodontids and *Fucaia goedertorum* (Barnes et al., 1995; Fitzgerald, 2010; Uhen, 2004). There are at least nine preserved teeth, including: a left (I1 or I2) and a right upper incisor (I2 or I3); the left upper canine or P1; the *in situ* roots of right p3; and five double-rooted postcanines, including at least one upper and one lower (figs 1–3, S1–S2). The left incisor has a broken apex, but otherwise displays intact labial and lingual enamel surfaces with no obvious abrasive wear (fig. 3A). The right incisor is abraded along two thirds of its lingual surface, but intact labially (fig. 3B).

All of the remaining teeth are heavily abraded with the consequent loss of all lingual enamel, except for a thin band along the base of the crown that was presumably located below the gum line (fig. 2). Between this basal band and the apex, the

lingual surface of each crown is deeply excavated and polished. Where preserved, the centre of the polished surface bears several deep, horizontal striations, the edges of which are themselves polished and rounded (fig. 2). Anteriorly and posteriorly, the abraded surface wraps around the crown, resulting in an hourglass-shaped labial wear pattern. The extent of labial wear varies, but in at least one tooth all of the enamel has been removed except for a centrally located, vertical strip (fig. 2B). The most heavily worn teeth, which are likely also the most posterior, have lost most of their crowns and are reduced to a basal band of enamel and a lingually excavated, low remnant of dentine (figs 2C, 3C).

Comparisons with Aetiocetidae and other marine mammals

The pattern and intensity of tooth wear in NMV P252567 is unique among Aetiocetidae. Besides the present material, tooth wear has been described in some detail for three aetiocetids, namely, *Aetiocetus cotylalveus*, *A. weltoni* and *Fucaia buelli* (Deméré and Berta, 2008; Emlong, 1966; Marx et al., 2015). In addition, teeth are preserved but have not been properly figured in *A. polydentatus* and *Morawanocetus yabukii* (Barnes et al., 1995). The enamel covering the crowns in all of these species lacks the heavy abrasion characteristic of NMV P252567. Several of the premolars and molars in the holotypes of *A. cotylalveus* (USNM 25210) and *A. weltoni* (UCMP 122900) instead show attritional wear, which has removed much or all of the accessory denticles (Deméré and Berta, 2008; Emlong, 1966). In addition, relatively minor apical abrasion is evident along at least the anterior portion of the tooth row in *A. weltoni*, and on both the premolars and molars of *A. cotylalveus*.

Tooth wear in *A. polydentatus* has not been described in detail, but (presumably attritional) wear facets seemingly occur at least on the posteriormost mandibular teeth (Deméré and Berta, 2008). Both attrition and apical abrasion also occur in *Fucaia buelli*, with extensive attritional wear facets occurring on the lingual surfaces of the upper premolars and molars of the type specimen (UWBM 84024; Marx et al., 2015). Too little is known about *Morawanocetus* to be sure about wear patterns in this species. Nevertheless, based on photographs, at least one of the posterior molars preserved with the holotype (AMP 01) displays strong apical and, possibly, attritional wear.

In general, the dental wear of NMV P252567 most closely resembles that of the bizarre-looking archaic mysticete *Mammalodon colliveri* and the extant walrus, *Odobenus rosmarus*, both of which show lingual abrasion and (microscopic) striations, and are considered to be benthic suction feeders (Fitzgerald, 2010; Gordon, 1984). Unlike NMV P252567, however, *M. colliveri* has small, peg-like incisors displaying heavy abrasion, and its dentition is generally even more heavily worn (Fitzgerald, 2010). Other marine mammals known to show heavy dental wear include the killer whale *Orcinus orca*, the beluga *Delphinapterus leucas*, the porpoises *Phocoena phocoena* and *Semirostrum ceruttii*, and the archaic beaked whale *Ninziphius platystris*. However, in orcas such wear generally consists of severe apical abrasion, possibly as a result of preying on sharks (Ford

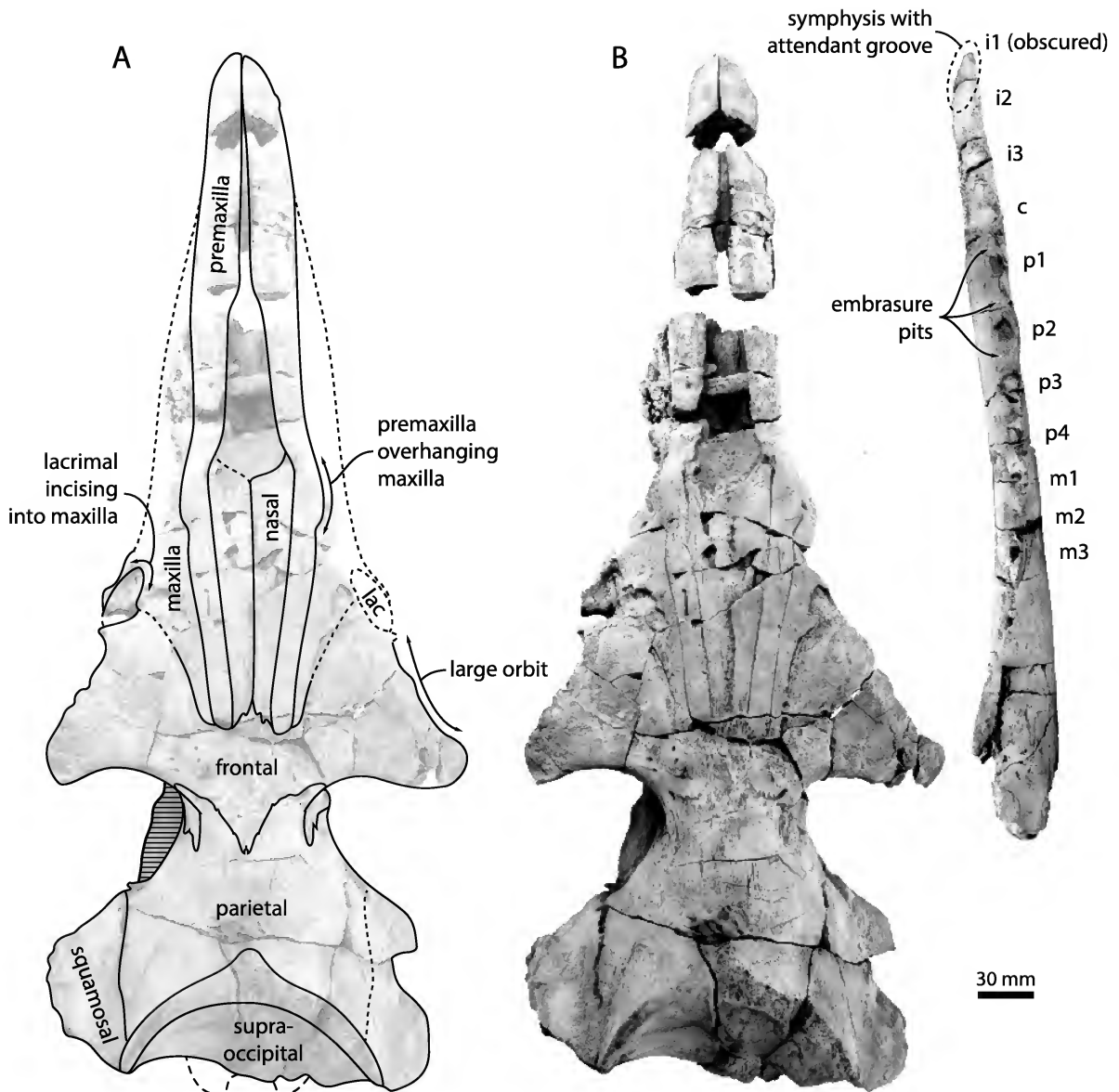


Figure 1. Diagnostic characteristics identifying NMV P252567 as an aetiocetid. A, explanatory line drawing of the skull; B, photograph of the skull (left) and mandible (right), both in dorsal view.

et al., 2011), while in belugas direct tooth-on-tooth occlusion results in a predominance of attrition (Fitzgerald, 2010; Struthers, 1895). By contrast, heavy wear in phocoenids and *N. platyrostris* may primarily reflect benthic foraging and the frequent ingestion of abrasive sediment (Lambert et al., 2013; Racicot et al., 2014), although more recent studies suggest that stem ziphiids may have foraged on epipelagic prey (Lambert et al., 2015).

Discussion and Conclusions

Feeding strategy of NMV P252567

The distinctive wear pattern of NMV P252567 provides insights into its likely feeding method. In particular, the pronounced lingual excavation of the crowns and attendant striations suggest that the insides of the teeth were subject to strong abrasive forces, such as repeated anteroposterior

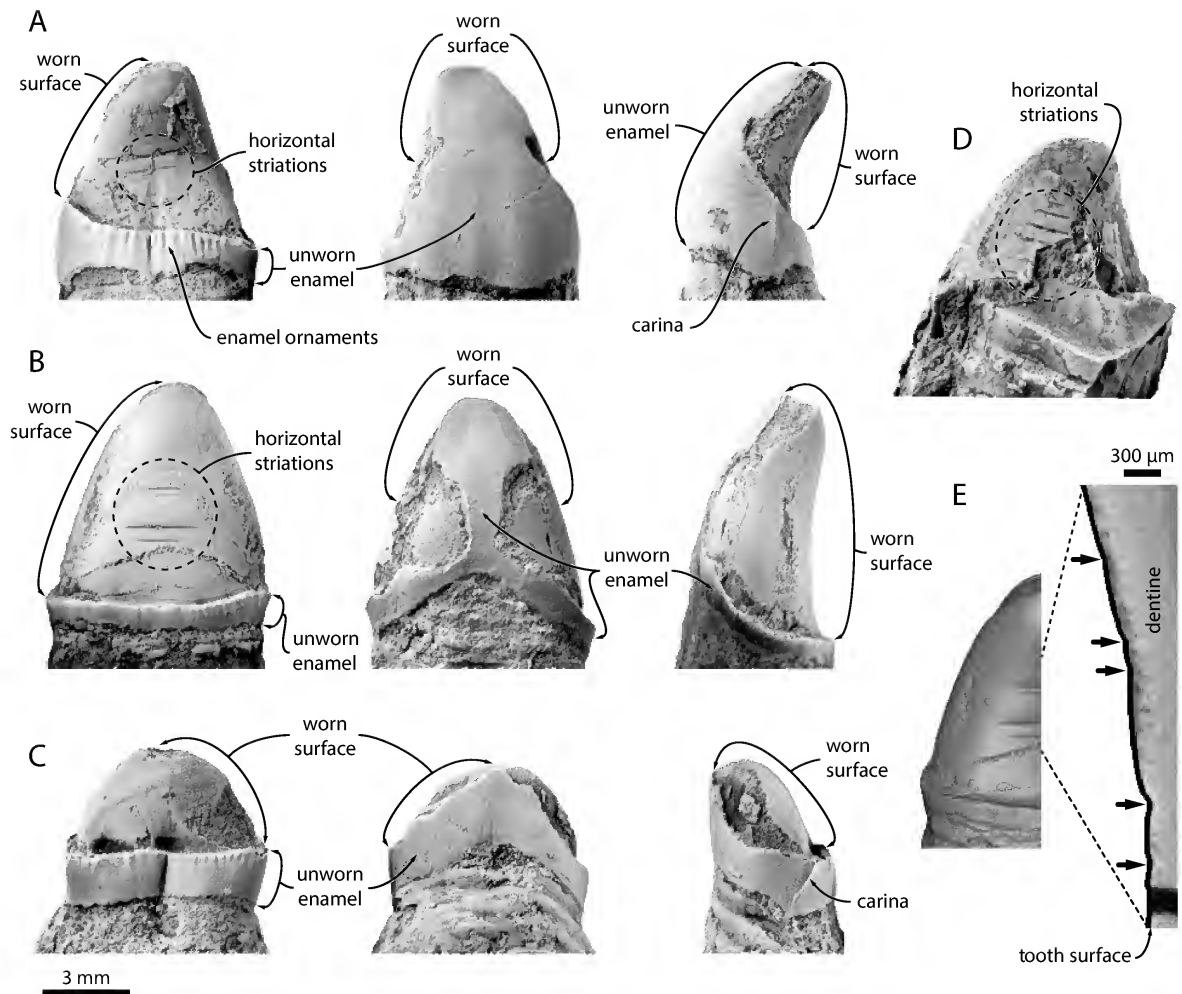


Figure 2. Wear patterns on representative teeth of NMV P252567, suggesting suction feeding in an aetiocetid. A, left upper canine or first premolar; B, double-rooted postcanine 1; C, ?lower double-rooted postcanine 2; D, ?lower double-rooted postcanine 3; E, micro-computed tomography cross section of postcanine 1, showing the depth and rounded edges of the horizontal striations (marked by large black arrows). A–C are shown in lingual, labial and anterior/posterior view, D in lingual view only.

(piston-like) movements of the tongue and/or flows of water laden with prey and sediment. The horizontal orientation of these forces is consistent with some form of (presumably benthic) suction feeding, as in *Mammalodon* and *Odobenus*, with the presence of lingual abrasion as far anteriorly as the incisors suggesting that suction was used for prey capture.

This interpretation holds irrespective of the age of the individual, as mature ontogeny would have exaggerated enamel wear without producing a heavy lingual bias or, particularly, the characteristic deep horizontal striations. Nevertheless, the intact enamel on the left upper incisor demonstrates that at least some of the anteriormost teeth were protected from wear, e.g. by being largely covered by gum tissue or by being located far

away from the main flow of prey and water. Baleen and tooth-assisted filter feeding can almost certainly be excluded, given that (i) baleen was most likely absent (see below) and (ii) the highly worn teeth would have been exceedingly poor at retaining small food particles. There is also no clear evidence for raptorial feeding, such as pronounced apical wear or dorsoventral shear facets, although such features may have been obliterated by heavy abrasion. At least facultative raptorial feeding may therefore have been possible.

We are not aware of a modern marine mammal showing a pattern of labial ‘hourglass’ wear that resembles that of NMV P252567. Nevertheless, the anterior, posterior and labial wear of the individual teeth is consistent with water and abrasive

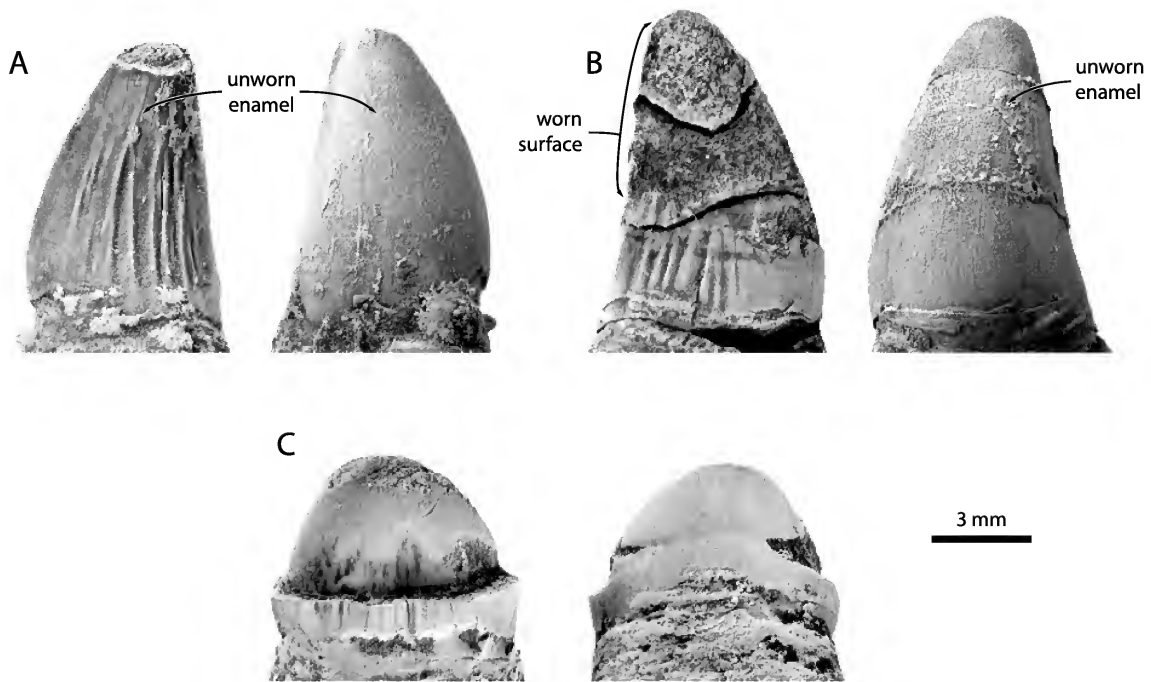


Figure 3. Additional teeth of NMV P252567. A, left upper incisor; B, right upper incisor; C, double-rooted postcanine 4. All teeth are shown in lingual (left) and labial (right) views. The lack or comparatively small degree of wear on the incisors suggests they may have been largely (left upper incisor) or partially (right upper incisor) enclosed within the gingiva, protecting them from the abrasive wear that affected the other teeth. A fifth double-rooted postcanine closely resembles postcanines 2 and 4 in terms of its wear, but is still partially encased in sediment and hence not shown here.

particles being forcibly expelled from the oral cavity through the diastemata. Similar water expulsion behaviour following suction has been observed in living species, such as pilot whales, belugas, leopard seals and Australian fur seals (Hocking et al., 2013; Hocking et al., 2014; Kane and Marshall, 2009; Werth, 2000a). During water expulsion, the jaws would likely have been held slightly open, causing the nearly occluding, interdigitating tooth rows to form a series of small gaps defined by the rims of the individual diastemata and the tips of the occluding upper or lower teeth. Sediment-laden water forced through these gaps would have abraded the enamel both along the rim of each diastema and on the immediately adjacent, labial portions of the tooth crowns. Over time, the labial wear surfaces would have enlarged into the hourglass wear observed here, possibly aided by the accidental, temporary retention of some sediment particles inside the lips after each water expulsion event.

Did aetiocetids have baleen?

Aetiocetids have previously been proposed as the most basal mysticetes to possess baleen, the key adaptation of modern whales. More specifically, the widespread occurrence of palatal nutrient foramina (in *Aetiocetus*, *Fucaia* and *Morawanocetus*), which in extant mysticetes supply the baleen

rack, has been used to infer the existence of an incipient baleen structure between or just lingual to the teeth (Deméré and Berta, 2008; Deméré et al., 2008). While such an interpretation is possible, it also remains untested: just as the origin of feathers in non-avian dinosaurs does not mark the beginnings of flight, so the appearance of palatal foramina in mysticetes need not indicate the presence of baleen. Instead, the foramina of aetiocetids could, for example, have supplied its immediate predecessor – namely, well-developed gums, the presence of which is indicated both by the strongly emergent teeth of early mysticetes (Deméré and Berta, 2008; Fitzgerald, 2010) and, possibly, the largely unworn incisor of NMV P252567.

The presence of palatal foramina in NMV P252567 cannot be determined owing to post-mortem breakage of the rostral margin. Nevertheless, this specimen is the first aetiocetid preserving clear evidence of its feeding strategy, and thus also the first test of the idea that baleen occurred in members of this family. In the case of NMV P252567, extreme lingual wear indicates that the teeth were directly exposed to strong abrasive forces uninhibited by adjacent keratinous tubules or plates. The deep horizontal striations in particular suggest that the teeth were affected by continuous, linear movements of the tongue and/or prey-laden water, which would have been hindered if baleen had shielded the inside of the tooth row.

The presence of baleen is made even less likely by the interdigitating dentition, as judged from the mandibular alveoli alternating with similarly-sized embrasure pits for the upper teeth (fig. 1). Interdigitating teeth also occur in *Fucaia goedertorum* (Barnes et al., 1995) and *Aetiocetus weltoni* (Deméré and Berta, 2008), and suggest a lack of space and risk of functional interference (i.e. teeth potentially damaging or disorganising the baleen rack) that speaks against the presence of functional baleen. Overall, we therefore conclude that NMV P252567 did not possess baleen and was hence incapable of filter feeding in a manner similar to modern mysticetes.

The condition of NMV P252567 reinforces previous, less decisive evidence against baleen in several other aetiocetids, such as the well-developed shear facets on the teeth of *Fucaia buelli* and the large size of the teeth in both *F. buelli* and *Morawanocetus* (Marx et al., 2015; Sawamura, 2008; Sawamura et al., 2006). Specifically, shearing in *F. buelli* would likely have posed a considerable risk of damage to the baleen rack after each bite, while the relatively elongate teeth of *Morawanocetus* (and, probably, *F. buelli*) result in short diastemata, abrogating the need for a baleen filter. Both of these observations rely on indirect evidence, but the difficulties in explaining how baleen could have functioned in these taxa are suggestive.

In extant baleen whales, tall lower lips, marked lateral bowing and longitudinal (alpha) rotation allow the mandibles to occlude on to the labial (rather than the ventral) surface of the baleen plates, thereby preserving the integrity of the rack (Lillie, 1915) (fig. 4). In *Aetiocetus* and *Fucaia*, essentially straight mandibles, a tall, straight coronoid process, embrasure pits, and the presence of attritional wear on the teeth (Deméré and Berta, 2008; Emlong, 1966) demonstrate that the lower jaw moved largely vertically and was positioned close to the upper jaw to enable tooth occlusion (fig. 4). An aetiocetid baleen rack would have been closely associated with the teeth, as judged from the position of the palatal foramina in *A. weltoni* and the juxtaposition of the rudimentary teeth and developing baleen in extant mysticete fetuses (Deméré et al., 2008; Ishikawa and Amasaki, 1995). As a result, aetiocetid baleen would have been constantly disturbed by mandibular contact.

Teeth could conceivably have acted as protective spacers between the jaws, allowing baleen to grow between or just medial to the upper teeth. However, the interdigitating dentition would still have resulted in considerable disturbance of the rack. It is also possible that the inherent flexibility of baleen would have allowed it to withstand compression, e.g. by folding away posteriorly as in extant bowhead whales (Werth, 2001; Werth, 2004). Unlike in bowhead whales, however, the presence of teeth in aetiocetids – both adjacent to the rack and coming from below – would likely have interfered with the folding process. We therefore suggest that, contrary to past proposals (Deméré and Berta, 2008; Deméré et al., 2008), the evolution of baleen likely only became feasible after the appearance of a laterally bowed mandible capable of clearing the baleen rack during mouth closure, and likely following the reduction or loss of emergent dentition (fig. 5).

Current model of baleen evolution

Current ideas on the origin of baleen argue for a direct transition from raptorial to bulk filter feeding, as seemingly exemplified by aetiocetids in their retention of functional teeth alongside features generally associated with filtering (Deméré et al., 2008). Besides the presence of (i) palatal foramina, these features include (ii) thin lateral margins of the maxillae; (iii) a relatively broad rostrum; and (iv) an unsutured, ligamentous mandibular symphysis. Laterally bowed mandibles, another feature claimed to be present in aetiocetids (Deméré et al., 2008), is not apparent in any of the specimens we examined (NMV P252567, fig. 1B; *Aetiocetus weltoni*, UCMP 122900; *Fucaia goedertorum*, LACM 131146), all of which instead possess effectively straight lower jaws.

While it is true that these traits facilitate bulk filter feeding in modern mysticetes (e.g. Lambertsen et al., 1995), their condition and function in archaic mysticetes is much less clear. As argued above, evidence from NMV P252567 and other aetiocetids speaks against the presence of baleen in this family, with the palatal foramina – the prime evidence for baleen – more likely supplying enlarged gums. Likewise, we see no direct link between thin lateral maxillary margins and filtering, and instead suggest that they may be a consequence of rostral broadening. The resulting increase in oral capacity would benefit both suction performance and filter feeding, so cannot be attributed to filtering alone (Fitzgerald, 2012; Werth, 2006). In any case, broad rostra are not characteristic of all filter-feeding whales: those of skim-feeding right whales are narrow and elongate, as essentially are those of the extant pygmy right (*Caperea marginata*) and even grey whales (*Eschrichtius robustus*).

Finally, the exact dental occlusion and tall, straight coronoid processes of *Fucaia* and *Aetiocetus* imply that longitudinal (alpha) rotation of aetiocetid mandibles was minimal compared with extant mysticetes, despite a ligamentous symphysis (Kimura, 2002; Lambertsen et al., 1995; Marx et al., 2015). Among extant mysticetes, a ligamentous mandibular symphysis enables extant balenopterids to rotate their bowed mandible along its long axis, thereby increasing oral volume during engulfment feeding (Lambertsen et al., 1995). By contrast, the mandible of aetiocetids is straight and constrained to largely dorsoventral rotation, rendering a mobile symphysis ineffective for increasing oral capacity (Arnold et al., 2005; Marx et al., 2015).

Alternatively, mandibular rotation may initially have enhanced control of the lower lip. In right whales, lateral lip rotation serves to create a flow channel lateral to the baleen rack during skim feeding (Lambertsen et al., 2005; Werth and Potvin, 2016). This feeding strategy requires a large filtration area, which in right whales is created by the arched rostrum and elongate baleen plates. Given its short, flat rostrum and erupted teeth, space limitations in the aetiocetid skull would have precluded this feeding mode. In grey whales, lip rotation appears to assist lateral suction feeding by creating an aperture for prey and water to be sucked into the oral cavity (Ray and Schevill, 1974). A similar behaviour in aetiocetids is conceivable, but the tall coronoid process would likely have prevented the opening of a wide enough gap.

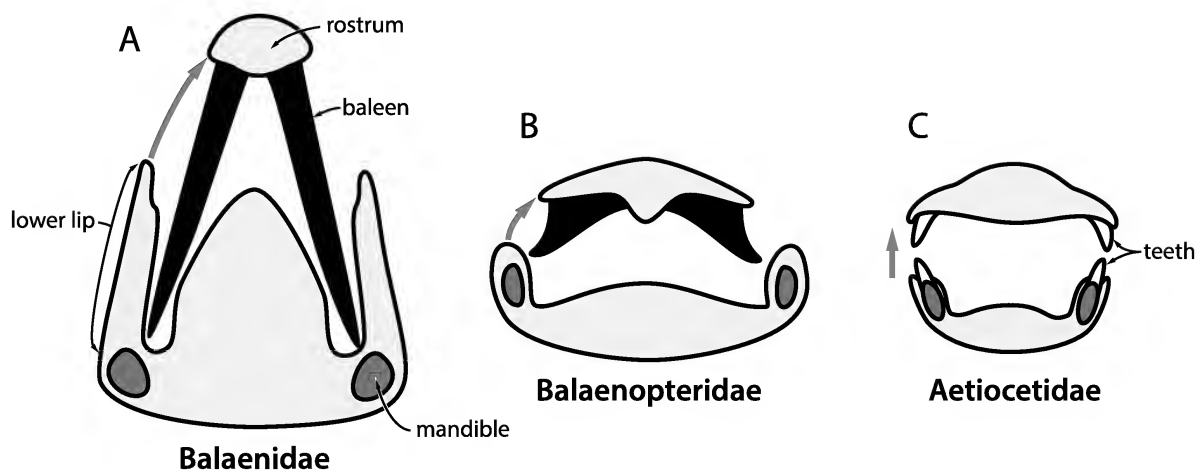


Figure 4. Cross section of the rostrum and lower jaws of A, a balaenid, B, a balaenopterid, and C, an aetiocetid, illustrating the relative movement of the mandible during jaw closure (red arrows). All drawings show the mouth slightly open. In right whales (A) and rorquals (B), the laterally bowed mandibles and/or tall lower lips rotate inwards on to the labial surface of the baleen plates, thereby leaving the rack intact. In aetiocetids (C), the movement of the mandible is mostly vertical and the upper and lower jaws need to approach each other enough to allow the teeth to occlude, thereby risking interference with any baleen present. A and B are adapted from Pivovarov (1979: fig. 3).

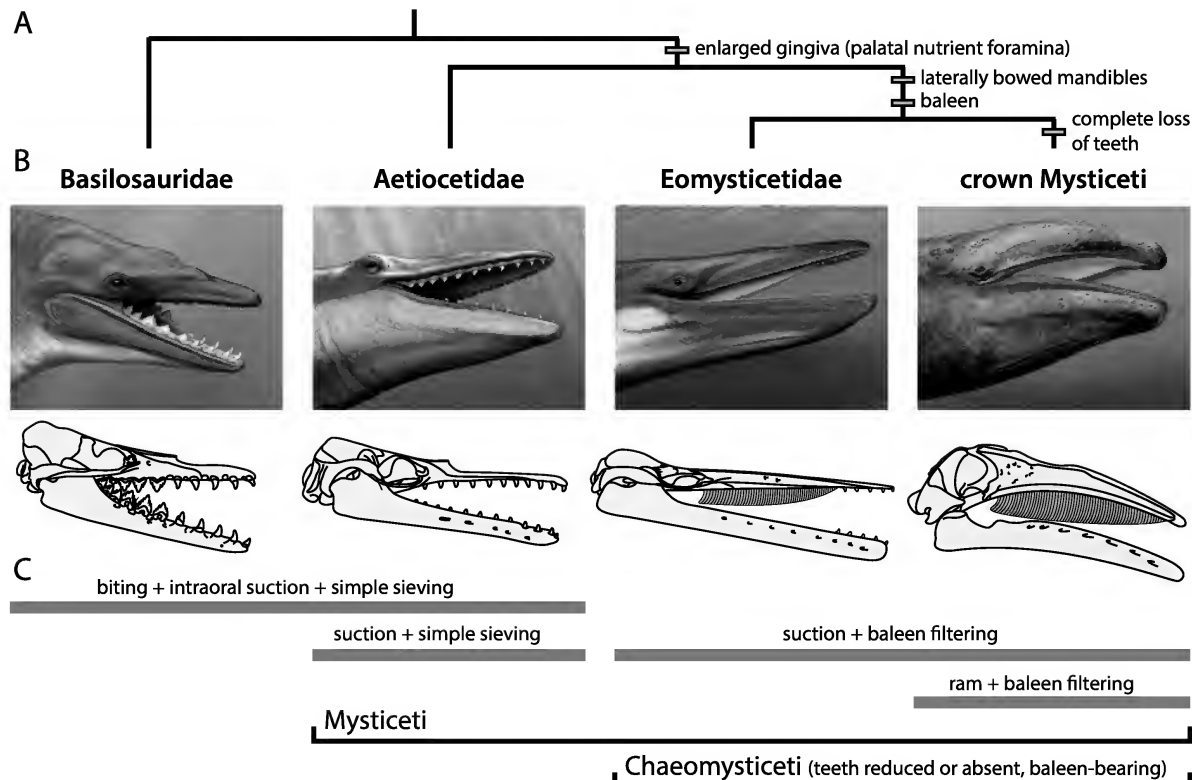


Figure 5. Suction feeding precedes baleen filtering in mysticete evolution. A, consensus tree of aetiocetid evolutionary relationships, based on all cladistic studies published to date (e.g. Deméré and Berta, 2008; Deméré et al., 2008; Fitzgerald, 2010; Geisler and Sanders, 2003; Marx and Fordyce, 2015; Steeman, 2007), showing major feeding-related synapomorphies; B, life reconstructions (top) and skulls (in lateral view) of a representative archaic mysticete (*Dorudon atrox*), aetiocetid (NMV P252567), eomysticetid (*Yamatocetus canaliculatus*) and extant suction feeding mysticete (grey whale, *Eschrichtius robustus*); C, inferred behaviours and feeding strategies. Life reconstructions by Carl Buell.

Overall, the function of the ligamentous symphysis in aetiocetids remains unclear. In particular, there is little evidence to suggest it was a specific adaptation to filter feeding. This point is emphasised further by the observations that, even among extant mysticetes, jaw rotation can be associated with suction feeding rather than filtration, and that an unsutured symphysis also occurs in a variety of other mammals, including – possibly – *Mammalodon* (Fitzgerald, 2010; Lieberman and Crompton, 2000).

An alternative model of baleen evolution

NMV P252567 makes a crucial contribution to the question of how baleen and bulk filtering first evolved. It is one of a limited number of fossil whales documenting the transition from raptorial to filter feeding; its cranial morphology disputes prior conjecture about the widespread presence of baleen in aetiocetids; and it provides the first reported evidence of suction feeding at the pivotal mysticete transition towards filter feeding and giant size. The ability to generate suction is fundamental to most marine vertebrates, and widespread among extant marine mammals, including pinnipeds and cetaceans (Hocking et al., 2013; Hocking et al., 2014; Kane and Marshall, 2009; Werth, 2000b; Werth, 2006). Nevertheless, up to this point it has rarely been associated with mysticete evolution, other than in reference to the highly unusual mammalodontids (Fitzgerald, 2010; Fitzgerald, 2012).

Suction is necessary when feeding underwater, where it enables the transport of food towards the back of the mouth for swallowing even in raptorial species that still employ teeth in prey capture (Werth, 2000b; Werth, 2006). This was likely already the case in archaic whales, soon after their initial transition to an aquatic environment. However, suction behaviour – whether for prey capture or intraoral transport – is generally difficult to demonstrate in fossils, since relevant osteological correlates, such as blunt, wide jaws (Werth, 2006) or a large hyoid apparatus (Bloodworth and Marshall, 2007; Heyning and Mead, 1996), are often either not preserved, or not always clearly developed, such as in the grey whale, *Eschrichtius robustus* (Kienle et al., 2015).

NMV P252567 offers an extremely rare insight into the evolution of suction behaviour and, along with *Mammalodon*, demonstrates a tendency for early mysticetes to evolve suction-based feeding strategies. There is currently no evidence that other aetiocetids relied on suction to a similar degree, although such a behaviour may be less apparent in animals that feed higher in the water column, and hence ingest less or no abrasive (i.e. wear-inducing) sediment. Nevertheless, given the apparently high degree of specialisation of NMV P252567 and the widespread occurrence of suction behaviour among extant marine mammals, it seems highly likely that aetiocetids were at least able to use suction for intraoral transport.

Use of suction and lack of baleen in aetiocetids suggests an alternative model – briefly hinted at by Arnold et al. (2005) – of how and why filter feeding first arose (fig. 5). Archaic mysticetes, including aetiocetids, likely inherited both a functional dentition and the ability to use suction for intraoral transport from their archaeocete ancestors (Werth, 2000b). Water ingested as a result of suction was expelled prior to swallowing (Hocking et

al., 2013; Hocking et al., 2014; Kane and Marshall, 2009; Werth, 2000a), with the prey either being physically held in place, or the teeth, jaws and surrounding soft tissues acting as a barrier, or simple sieve, retaining food items inside the mouth (Bloodworth and Marshall, 2005; Hocking et al., 2013). Some of these early whales, including NMV P252567, *Mammalodon* and the ancestor of modern mysticetes, honed their suction capabilities to the point where they became able to capture prey, and we suggest that it was this transition, not filter feeding, that ultimately initiated tooth loss in the chaemysticete lineage.

Among both extant (sperm whales, beaked whales and certain delphinids) and extinct odontocetes (e.g. *Australodelphis*, *Odobenocetops*), capture suction feeding strongly correlates with a reduced dentition (Werth, 2000b; Werth, 2006), and the same may plausibly have been the case in mysticetes. This scenario avoids potential problems of functional interference between a working dentition and incipient baleen (Marx et al., 2015), and explains how teeth could have been lost without impacting on foraging success. Further, a loss of functional teeth prior to the origin of baleen coincides with evidence of foetal development from extant mysticetes, which shows that baleen growth only initiates once the tooth buds have already started to degrade (Ishikawa and Amasaki, 1995; Karlsen, 1962). It is possible that teeth and baleen nonetheless co-occurred in some archaic chaemysticetes, as shown by eomysticetids bearing shallow alveoli and, possibly, teeth (Boessenecker and Fordyce, 2015); however, the dentition in these taxa was already reduced. We also note the similar anterior positioning of teeth in eomysticetids and extant suction-feeding odontocetes like the beluga, and the delphinids *Grampus* and *Globicephala*.

Suction for capture limited the maximum size of prey that could be taken, and furthermore would have enabled the ancestors of modern mysticetes to gather small prey items in bulk; however, the absence of specialised filtering teeth, such as those of the extant crabeater (*Lobodon*) and leopard seals (*Hydrurga*), would have permitted the inadvertent expulsion of small food particles prior to swallowing, as observed in trials with California sea lions (*Zalophus californianus*) (Hocking et al., 2013). This problem was eventually solved by the elaboration of the gingiva, first potentially as a grasping (Miller, 1929) and, ultimately, a filtering apparatus – i.e. baleen. A similar condition exists in the extant Dall's porpoise *Phocoenoides dalli*, which supplements its rudimentary dentition with a series of 'gum teeth' that are structurally similar to the early growth stages of baleen (Miller, 1929). As Miller (1929: 4) himself observed: "These resemblances are so important that we are probably justified in regarding the gingival and dental structures of *Phocoenoides* as representing anatomical stages closely parallel to those through which the corresponding parts in the toothed ancestors of the Mysticeti must have passed."

The feeding strategy of the earliest baleen-bearing whales would initially have been a form of intermittent or continuous suction filter feeding, as inferred for a range of extinct cetotheriids (El Adli et al., 2014; Gol'din et al., 2014), and still observed in the extant grey whale, *Eschrichtius robustus* (Ray and Schevill, 1974). However, with baleen now in place, other methods of filtering no longer reliant on suction also became

possible, including the highly specialised skim (Werth and Potvin, 2016) and lunge feeding (Lambertsen et al., 1995) strategies of extant right whales and rorquals, respectively.

Our new model is consistent with all available palaeontological, developmental and behavioural evidence, but will benefit from further research effort. This might include an investigation of dietary stable isotopes, to determine at what trophic level aetiocetids were feeding (e.g. Clementz et al., 2014); an increased focus on the oldest (Late Eocene–Early Oligocene) mysticetes, to test for evidence of suction feeding in early chaeomysticetes (e.g. tooth wear), or further evidence regarding baleen in aetiocetids, e.g. in the form of actually preserved traces (e.g. Esperante et al., 2008; Gioncada et al., 2016); and further studies of the feeding strategies of extant marine mammals, to determine possible modern analogues of archaic mysticetes. Overall, our findings suggest that suction behaviour was fundamental to the evolution of baleen and filtering, and thus a crucial early innovation that helped to trigger the rise of the largest animals on Earth.

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Figure S1. Upper left canine or first premolar of NMV P252567.

- **Custom View 1:** Lingual view showing horizontal striations.
- **Custom View 2:** Labial view showing hourglass wear eroding the enamel surface.
- **Custom View 3:** Anterior view showing erosion of the lingual surface above the gum line.

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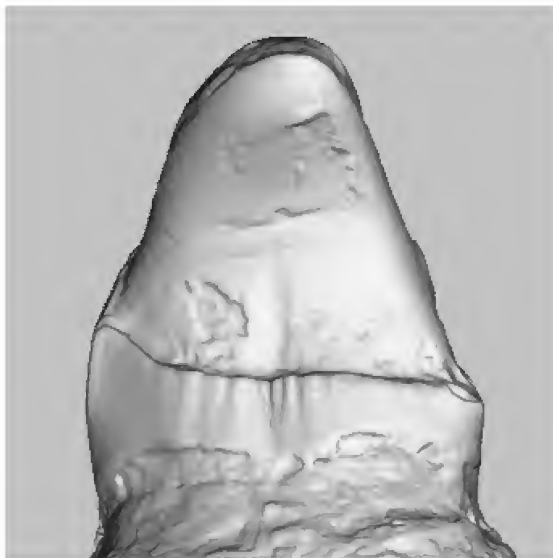


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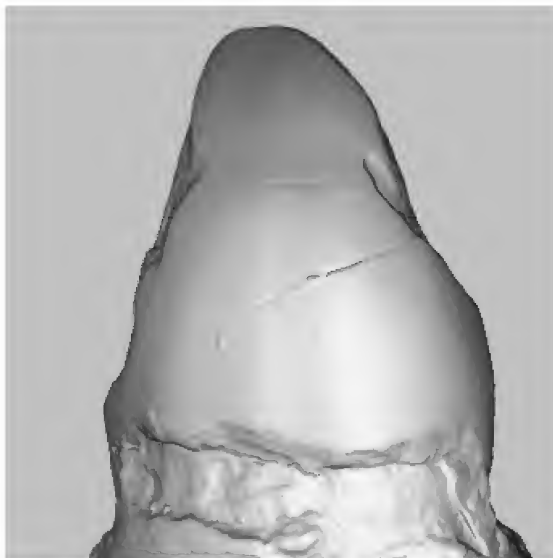


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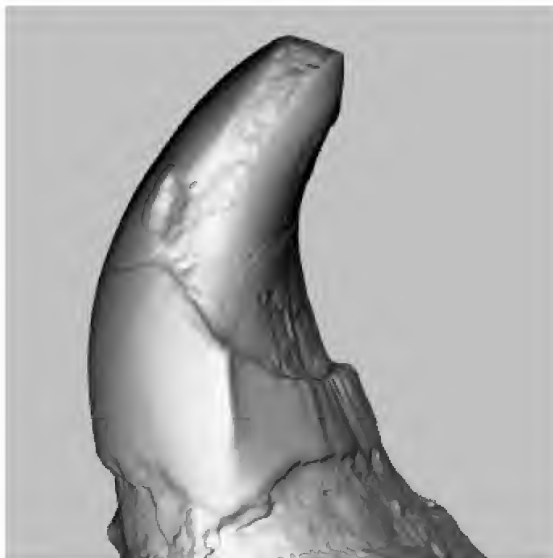


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Figure S2. Double-rooted postcanine 1 of NMV P252567.

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- **Custom View 2:** Labial view showing hourglass wear eroding the enamel surface.
- **Custom View 3:** Profile view (anterior or posterior) showing erosion of the lingual surface above the gum line.
- **Custom View 4:** Close-up view of the horizontal striations showing polished edges.

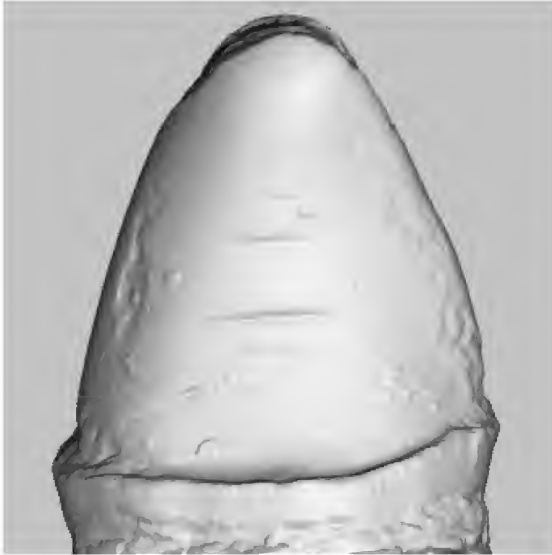


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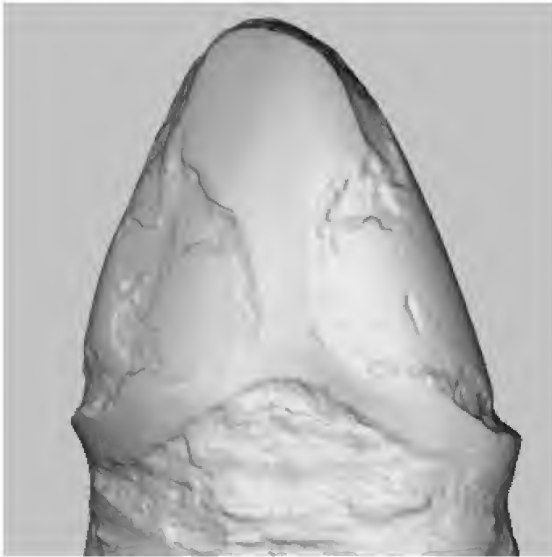


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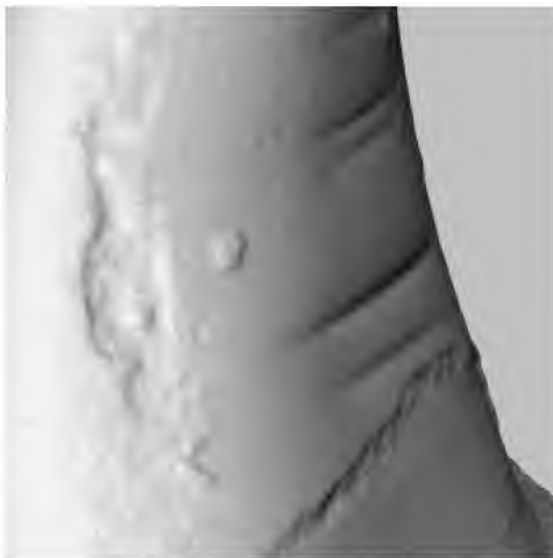


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